

LATE EOCENE-OLIGOCENE NONMARINE MOLLUSKS OF THE
NORTHERN KISHENEHN BASIN, MONTANA AND BRITISH COLUMBIAHAROLD G. PIERCE¹

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ABSTRACT

The Kishenehn Basin is a narrow, asymmetric graben, developed during an episode of crustal extension occurring from middle Eocene to early Miocene time (ca. 49–20 Ma). The Flathead listric normal fault system defines the northeast margin of the basin. The southwest margin is either bounded by antithetic normal faults or is overlapped by Kishenehn Basin strata. High rates of basin subsidence and synextensional sedimentation resulted in an immense thickness of middle Eocene-early Miocene strata (stratigraphic thickness, ~5000 m) and a relatively uninterrupted depositional record. Provenance and paleocurrent studies indicate that the ancestral Livingston, Lewis, and Clark ranges to the east contributed not only vast amounts of detritus to the Basin, but also ample runoff that included seasonal snow-melt. Sediment ages of outcrops within the basin are linearly banded, with the course of the Flathead River exposing late Eocene-early Oligocene sediments (Chadronian-Orellan NALMA's), and with the oldest sediments on the southwest and youngest on the east margins of the basin, respectively. An unnamed tephra at the north end of the basin provides a date of 33.0 ± 1.0 Ma (early Oligocene, Orellan NALMA).

The molluscan fauna is extremely diverse, 55 taxa (35 terrestrial, 20 aquatic), of which 32 taxa are new, and seven are revised taxonomically. This fauna is clearly divisible into three Groups. Group I is a relict tropical wet fauna, existing along waterways in the sheltered environment of the basin. It may typify the pre-middle Eocene (early Duchesnean NALMA) tropical climate of the Western Interior of North America. Modern analogs of these taxa are found in the Caribbean, Central and South America. Group II is a semitropical, semiarid fauna that developed after the climatic changes of the middle Eocene. Modern analogs are found in a band from the north coast of the Gulf of Mexico across the southern United States and northern Mexico to Southern and Baja California. Essentially 100% of the Group I and II analog taxa are now extra-limital, displaced to the south. Group III taxa developed in uplands along the east margin of the basin. Modern analogs of these taxa are common in the east-central United States. The coexistence of these climatically disparate groups of mollusks is a reflection of the large paleotopographic relief that existed between the basin floor and the eastern mountain peaks, which rose at least 2,000 meters above the basin floor, and permitted microclimates that varied from arid subtropical in the basin to humid temperate in the uplands. At the older localities, Group III taxa were, probably, transported into the basin by run-off from the mountains, but during the climatic cooling of the latest Eocene-early Oligocene, Groups I and II taxa were replaced by Group III taxa in the low-lands. Group III analog taxa are 87% endemic, although their modern centers of distribution are displaced eastward into an area of greater precipitation.

The following taxa are described herein as new: Bivalvia: Veneroidea: Sphaeridae—*Sphaerium discus*. Gastropoda: Archaeogastropoda: Ceresidae—*Tozerpina buttsi parva*, *T. lentis*; Helicinidae—*Lucidella salishora*, *L. columbiana*; Mesogastropoda: Hydrobiidae—*Tryonia russelli*, *Cincinnati? bowmanana*, *Fluminicola calderense*; Valvatidae—*Valvata procera spatiosa*; Basommatophora: Planorbidae—*Helisoma triangulata*, *Planorbella fordensis*, *Biomphalaria spira*, *Menetus textus*, *Menetus hilli*; Lymnaeidae—*Lymnaea bowmanana*, *L. lacerta*; Stylommatophora: Succineidae—*Oxyloma? kintlana*, *Omalonyx cocleare*; Pupillidae—*Pupoides costatus*, *Gastrocopta kintlana*, *G. akokala*, *Vertigo consteniusi*, *V. doliara*, *V. micra*; Valloniidae—*Vallonia kootenayorum*; Urocoptidae—*Holospira tabrumi*,

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H. beardi, *Coelostemma dawsonae*; Polygyridae—*Praticolella lucifera*, *Ashmunella*(?) sp.; Oreoheliciidae—*Oreohelix dawsonae*, *Radiocentrum kintlana*; Humboldtianidae—*Skinnerelix rothi*; Helminthoglyptidae—*Xeranionta constenii*. The following constitute new taxonomic combinations: *Tozerpina* “*Triodopsis*” *butsi* (Russell, 1956), *Omalonyx* “*Binneya*” *antiqua* (Russell, 1956), *Haplotrema* “*Anguispira*” *simplex* (Russell, 1956), *Lymnaea* “*Stagnicola*” *newmarchi* (Russell, 1952), *Biomphalaria* “*Planorbis*” *kishenensis* (Russell, 1952), *Valvata* “*Gyraulus*” *procera* (Russell, 1952).

KEY WORDS: Eocene-Oligocene, nonmarine mollusks, paleoclimates, structure, crustal extension

INTRODUCTION

General Introduction.—This paper is but a part of a comprehensive, multidisciplinary study of the Kishenehn Basin, a complex, narrow, half-graben filled by Tertiary sediments, about 150 km in length, trending north to northwest across the border between British Columbia and Montana (Figs. 1, 2). In this paper, we deal with the geology and with the mollusks of only the northern portion of the Kishenehn Basin, that part exposed by the North Fork of the Flathead River in both British Columbia, Canada and Montana, U.S.A. The mollusks of the Middle Fork portion of the Kishenehn Basin, which are exposed by the Middle Fork of the Flathead River and are exclusively in Montana, and the ostracods of the entire basin, will be the subject of future papers (our next report). In this paper, Constenius is responsible for the structure and stratigraphy, whereas Pierce is responsible for the molluscan paleontology.

Recently, there has been renewed interest in the late Eocene-Oligocene—early Miocene nonmarine mollusks of the northern Rocky Mountains. A first report on the Kishenehn Basin by Daly (1912) included a short list of freshwater mollusks, examined by T. W. Stanton, from a locality just north of the International Boundary. Stanton felt their age could be as old as Eocene. MacKenzie (1916:36–37) reported observations by W. H. Dall on freshwater mollusks collected at an unstated location in the Kishenehn Basin. Dall, too, suggested a possible Eocene age for these mollusks. This was followed by the first comprehensive investigation by Russell (1952, 1956, 1964), along the North Fork of the Flathead River, who proposed an age of latest Eocene. Ross (1959:68–72) reported on mollusks identified by T. C. Yen and D. W. Taylor from both the North and Middle Forks of the Flathead River, but with considerable disagreement as to age. While Taylor concurred with an Eocene or Oligocene age, Yen regarded them as “possibly of late Tertiary age” to as young as early Pleistocene (*vide* Ross, *loc. cit.*).

Since then, several other faunas in western Montana have received detailed appraisal (Table 1, Fig. 3). Roth (1986) studied the Eocene-Oligocene Three Forks molluscan local fauna (l.f.) of Jefferson and Gallatin Counties and the Oligocene Deep River l.f. of Meagher County (Roth and Emberton, 1994). Roth was first to comment extensively on the extralimital nature of these faunas as part of his study of the Three Forks l.f. (*loc. cit.*). Pierce investigated the late Oligocene-Miocene Cabbage Patch l.f. of Granite and Powell Counties (Pierce and Rasmussen, 1992; Pierce, 1992, 1993), and the small Miocene Flint Creek l.f. of Granite County (Pierce and Rasmussen, 1989). Evanoff briefly mentioned the mollusks of the White River l.f., late Eocene-Oligocene, of the Douglas County, Wyoming area (Evanoff et al., 1992). Pierce made preliminary comments on a reconnaissance of that portion of the Kishenehn Basin exposed by the Middle Fork of the Flathead River (Constenius et al., 1989).

Previous investigations of the molluscan faunas of the Kishenehn Basin/Flathead River, except those of Russell (1952; 1956), had been superficial, or dealt

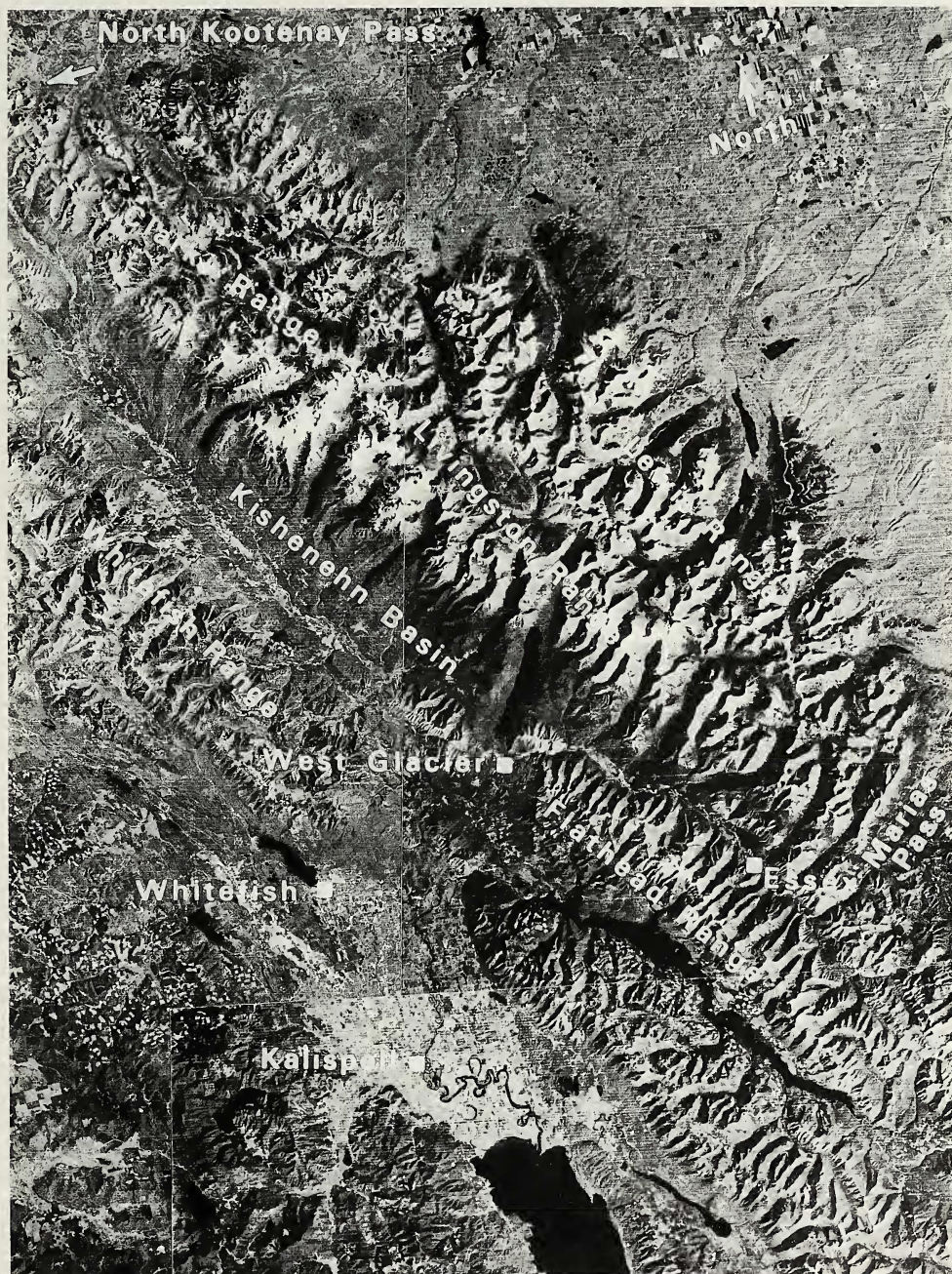


Fig. 1.—Landsat image of parts of northwest Montana, southeast British Columbia, and southwest Alberta, showing mountain ranges and other geographic features surrounding the Kishenehn Basin. See Figure 2, upper right, for index map.

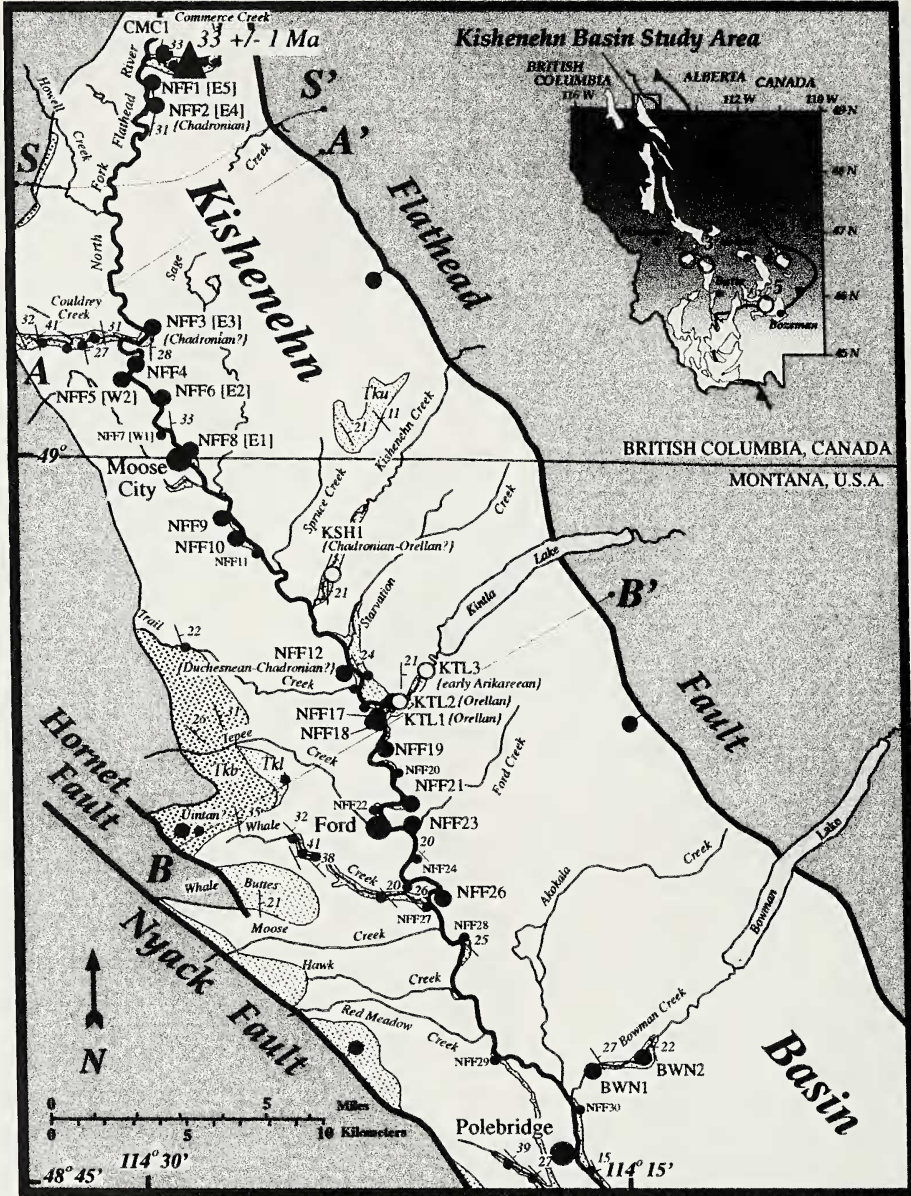


Fig. 2.—Geologic index map showing: (1) the location of the Kishenehn Basin and its setting with respect to other Tertiary basins of western Montana, and to the leading-edge of the Cordilleran fold-thrust belt (inset, upper right); and, (2) fossil localities of the North Fork region of the Kishenehn Basin. Numbered western Montana basins are (1) Kishenehn Basin, (2) Flint Creek Basin, (3) Deer Lodge Basin, (4) Smith River Basin, and (5) Three Forks Basin. Outcrops of Kishenehn Formation barren of invertebrate or vertebrate fossils shown as small gray dots and labeled with small-sized letters. Invertebrate localities, including some with vertebrate fossils shown as large gray dots and large-sized letters. Vertebrate localities shown as large open circles, large-sized letters and designated land mammal age.

Table 1.—*Molluscan local faunas (l.f.) of the mid-Tertiary Western Interior.*

Molluscan Local Fauna (l.f.)	NALMA	Map no.	Reference
Flint Creek l.f. Granite Co., MT	e. Barstovian?	5	Pierce and Rasmussen, 1989
Cabbage Patch l.f. Granite and Powell Co's., MT	Arikareean	4	Pierce and Rasmussen, 1992 Pierce, 1992; 1993
Deep River l.f. Meagher Co., MT	Orellan- Arikareean	3	Roth and Embeton, 1994
Kishenehn l.f. Flathead Co., MT and S. Br. Col.	Chadronian- Arikareean?	1	Russell, 1952; 1956 This paper
White River l.f. Converse Co., WY	Chadronian- Orellan		Evanoff et al., 1992
Three Forks l.f. Jefferson and Gallatin Co's., MT	Uintan- Chadronian	2	Roth, 1986

with only a small part of the basin. During our studies, a richly diverse molluscan fauna, representing multiple climatic regimes, ranging from tropical to temperate, was collected from many localities exposed by both the North and Middle Forks of the Flathead River and their tributaries. The diversity was so great, both taxonomically and environmentally, that a decision was made to report first on the generally younger(?) sediments and molluscan fauna found along the North Fork of the Flathead River. Even so, this paper deals with 55 molluscan taxa, of which 32 are new.

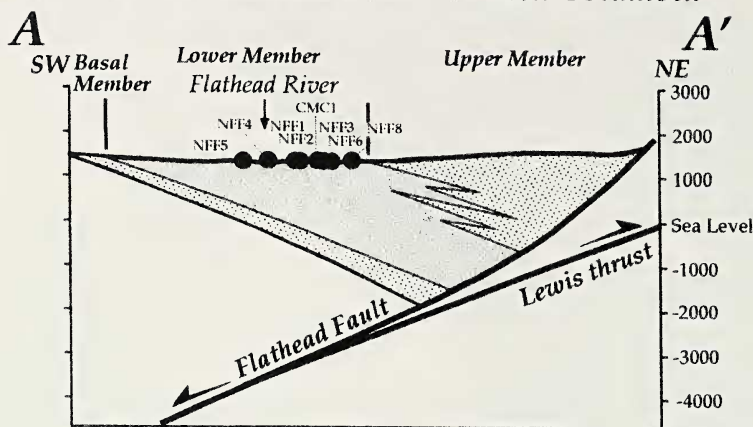
This study focuses on the molluscan fauna recovered from ten localities in the North Kishenehn Basin along the North Fork of the Flathead River and its tributaries in Flathead County, Montana and eight localities in southern British Columbia, Canada (Fig. 2). The southernmost Montana locality is along Bowman Creek (BWN-2), about 3.2 km above its confluence with the North Fork. The northernmost locality, in British Columbia, is along Commerce Creek (CMC-1), about one km above its confluence with the North Fork. With the exception of the Kintla Creek-Carnegie (Montana) locality (KTL-1), the localities are all cut banks along the North Fork of the Flathead River or its tributaries. Five of the eight localities in British Columbia are at, or very near, Russell's localities (1964: 541–542) and Russell's locality designations are used informally, e.g., E-2 (NFF-6), W-2 (NFF-5), E-3 (NFF-3), E-4 (NFF-2), and E-5 (NFF-1), without the implication that these are the identical localities studied by Russell. For location data and a description of each locality, refer to Appendix 1.

The following abbreviations are used: CMNH or CM, Carnegie Museum of Natural History; KUMIP, University of Kansas Museum of Invertebrate Paleontology; P***, reference collection of H. G. Pierce; NALMA, North American Land Mammal "Age"; l.f., molluscan local fauna; Ma (Mega-annum), 10^6 years before present.

Geologic Setting.—The Kishenehn Basin is part of a network of late Paleogene grabens that formed during a post-Laramide episode of crustal extension that affected western North America from southern British Columbia to central Mexico (Coney, 1987; Dickinson, 1991; Constenius, 1996). This chain of grabens, of which the Kishenehn Basin is one of the northern-most, are superposed on the Cordilleran foreland fold and thrust belt, and formed when the thrust belt collapsed during a middle Eocene to early Miocene (ca. 49–20 Ma) episode of crustal

Kishenehn Basin

North Fork Flathead River - British Columbia



North Fork Flathead River - Montana

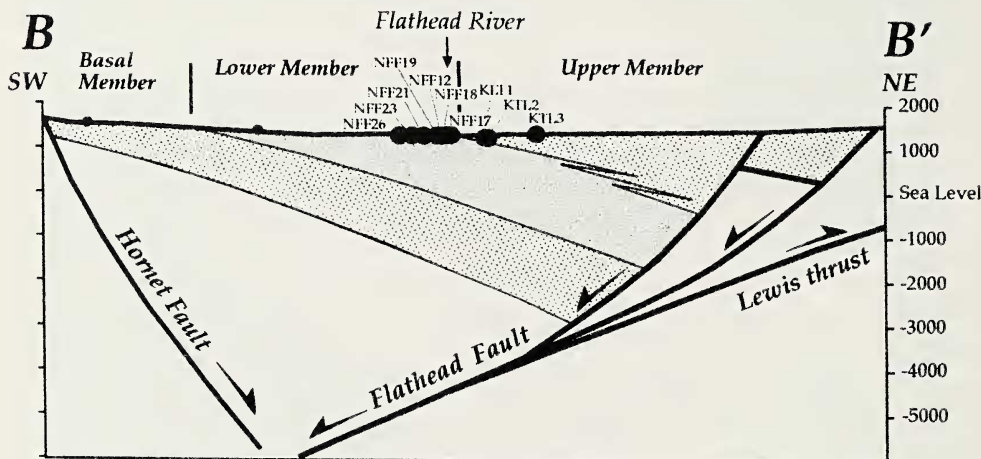


Fig. 3.—Geologic cross sections of the Kishenehn Basin showing relationship of basin stratigraphy to localities discussed in text. Note limited stratigraphic range of Kishenehn fossil localities. Sources of data include the following: Jones, 1969; McMechan, 1980; and, Constenius, 1981. Location of cross sections shown on Figure 2.

extension. Consequently, extensional basins developed within this allochthonous terrain are rooted to preexisting thrust-fold structures and the sedimentary record of late Paleogene crustal spreading is found in thick, nonmarine, basin-fill assemblages. These linkages are reflected in the modern Basin and Range landscape of southeastern British Columbia and western Montana in which the north to northwest-trending, elongate basins and congruous mountain ranges parallel the front of the fold-thrust belt (Figs. 1, 2).

The Kishenehn Basin, situated southwest of the Lewis Thrust salient, is a narrow, asymmetric graben 150 km long and varies from 2 to 13 km wide (Constenius, 1982). Physiographically, the basin is surrounded by the rugged alpine peaks of the Lewis, Livingston and Clark ranges to the northeast, and by the comparatively lower relief MacDonald, Whitefish, Apgar-Belton Hills, and Flathead ranges to the southwest. The basin is divided into two distinct regions, the North Fork and Middle Fork, by the Flathead River drainage. Cenozoic sedimentary rocks that fill this intermontane basin consist of two stratigraphic assemblages, late Paleogene rocks of the Kishenehn Formation and Quaternary glacial and alluvial sediments.

The Flathead listric normal fault system, the master structure that controlled basin origin, borders the Kishenehn Basin to the northeast and is prominently defined in the landscape as the line of transition from subdued valley floor to precipitous mountain topography. Estimates of maximum dip-slip on the Flathead Fault are on the order of 15 km (Constenius, 1988). The southwest basin margin is variously bounded by normal faults antithetic to the Flathead system, such as the Nyack and Hornet faults, or it is overlapped by strata of the Kishenehn Formation (Figs. 2, 4). Subsidence along these faults created an asymmetric graben containing up to 3,400 m (vertical thickness) of nonmarine, late Paleogene sedimentary rocks of the Kishenehn Formation. Because of the growth-fault sedimentary geometry of the basin, estimates of the maximum preserved stratigraphic thickness range from 4,750 m to more than 5,000 m (Jones, 1969; Constenius, 1981, 1988). Relict high-elevation basin-fill deposits indicate that at least 400 m (vertical thickness) of Kishenehn Formation has been removed by post middle Miocene erosion (Price, 1965; Jones, 1969; Constenius, 1981).

The structural position of the Kishenehn Basin with respect to the Lewis Thrust salient reflects the common fault surface that accommodated late Cretaceous-early Eocene crustal contraction followed by middle Eocene-early Miocene extension (Figs. 1, 4, 5) (McMechan, 1981; Constenius, 1982). The linkage between the Lewis Thrust and Flathead Fault is seen in the position and symmetry of the fault systems. Details of the structural interactions of these linked contractile-extensional fault systems are reviewed by Bally et al. (1966), McMechan (1981), and Constenius (1982, 1988, and 1996). Importantly, the Flathead Fault has been identified as a southwest-dipping listric normal fault that merges with the reactivated segment of the Lewis Thrust. The fault dips $\sim 40\text{--}50^\circ$ southwest near the surface and flattens at depth (Figs. 4, 5). Interpretation of seismic reflection data suggests that the Lewis-Flathead fault surface is layer-parallel in basal Cambrian strata. Consequently, the detachment horizon dips about $2\text{--}3^\circ$ southwest paralleling an undeformed autochthonous crystalline basement (Bally et al., 1966; Yoos et al., 1991; Van der Velden and Cook, 1994).

The synextensional nature of the Kishenehn Formation has been established using sedimentary structures, facies relationships, provenance, paleocurrent directions, geophysical data, and stratal growth geometries (Constenius, 1981, 1982, 1988, 1989; McMechan and Price, 1980; McMechan, 1981). Synextensional sedimentary sequences display stratal growth relationships, that is, a systematic thickening of strata toward the basin-bounding listric normal fault and a gradual flattening of dip in successively younger units (Dahlstrom, 1970; McMechan and Price, 1980). The strong rotational control on sedimentation associated with listric normal faulting results in a half graben or asymmetrical graben with a wedge-shaped sedimentary prism (Figs. 4, 5). The Kishenehn Basin is a half- or asym-

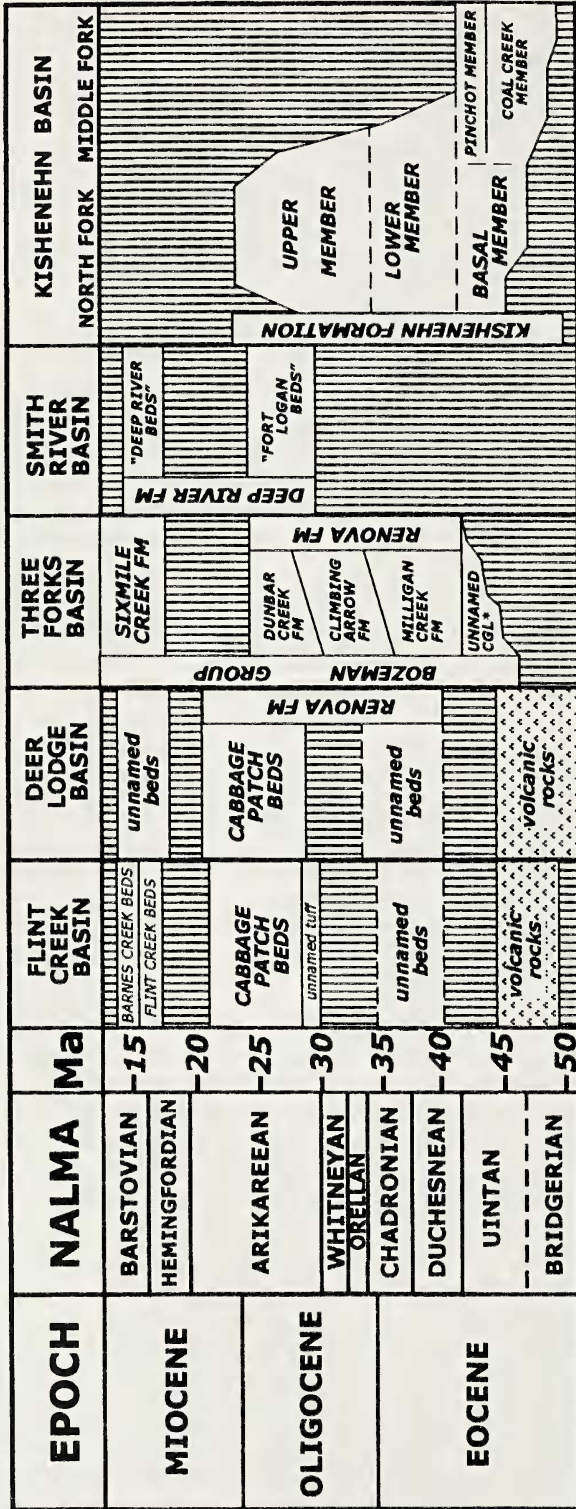


Fig. 4.—Stratigraphic correlation chart of selected Tertiary basins in western Montana. Adapted from Pierce and Rasmussen, 1992a.

metric graben in the central and northern parts of the basin where this study focused on invertebrate paleontology. The dip of the Kishenehn Formation strata in the North Fork region ranges from $\sim 35\text{--}40^\circ$ in the lowest Duchesnean-age beds and decreases systematically upsection and toward the Flathead Fault to $\sim 20\text{--}25^\circ$ (Fig. 2) (Constenius, 1981; McMechan, 1981). Hence, preserved in these middle Eocene to early Miocene synextensional strata is a record of $35\text{--}40^\circ$ of total rotation of the hanging wall; $\sim 10\text{--}20^\circ$ of growth-fault-related rotation, and $\sim 20\text{--}25^\circ$ post-depositional rotation. Progressive rotation of beds indicates that displacement along the Flathead Fault system was synchronous with Kishenehn sedimentation.

The distribution and age of Kishenehn strata preserved in the basin is not solely related to down-dropping and rotation on the basin-bounding faults. Rather, subtle warping of the Earth's crust has imparted a regional northward tilt to the basin such that seismic mapping of the top of the crystalline basement shows considerable deepening to the north-northwest. Although the dip-rate is small, on the order of 1–2 degrees ($17\text{--}34$ m/km) over a distance of 100 km or more, the effect is large. As a consequence, middle Eocene (Uintan) rocks are exposed at the south end of the basin (Middle Fork region), in contrast to late Eocene (Duchesnean/Chadronian) rocks in the north end of the basin in Canada. Without this tilt we would expect a younger basin fill assemblage, perhaps Duchesnean/Chadronian age or younger, on top of the Pinchot Creek Member in the Middle Fork region (Fig. 3). The level of erosion in relation to regional arching of the basement is also expressed in the level of erosion of the fold-thrust belt. For example, in the hanging wall of the Lewis Thrust sheet, the youngest rocks preserved on the south end of the thrust salient are middle Proterozoic Belt Supergroup. Whereas on the north end in Canada, rocks as young as Devonian are preserved. Geochemical data on the thermal maturity of Kishenehn oil shales and coals provide direct evidence of a deeper level of erosion (i.e., more overburden removed) in the south end of the basin as compared to the north end (Curiale et al., 1988).

Previous age determinations of the Kishenehn Formation concluded that the formation was late Eocene to early Oligocene in age (Russel, 1954, 1964; Hopkins and Sweet, 1976; McMechan, 1981). These studies relied on fossil mammals, mollusks, leaves, and pollen from exposures in Canada. Unpublished studies of palynomorphs by the U.S. Geological Survey suggested a late-middle(?) Eocene to late Eocene and late Eocene-Oligocene(?) age for Kishenehn strata from the Middle Fork and North Fork regions, respectively (R. H. Tschudy, written communication, 1979; D. J. Nichols, written communication, 1980). In a reconnaissance paleontologic study, Constenius et al. (1989) noted inconsistent paleontologic and geochronologic age estimates ranging from late Eocene to early Miocene. They postulated that the Kishenehn was deposited over a long time span and may have been a refugium with a mixture of faunal and flora types.

Recent collection and study of mammalian fossils indicates that Kishenehn strata exposed in the North Fork region are mainly late Eocene-early Oligocene (Duchesnean-Arikarean; $\sim 41\text{--}24$ Ma) in age (Figs. 2, 3), and a middle Eocene age (Uintan; $\sim 48\text{--}42$ Ma) for Kishenehn strata in the Middle Fork region (M. R. Dawson, personal communication, 1998) is indicated. Discovery of a single large lobate leaf fossil of *MacGinitea* sp. in basal beds of the Kishenehn Formation suggests that part of the North Fork section may be as old as middle Eocene in age. Geochronologic analysis of two tephras yielded $^{40}\text{Ar}/^{39}\text{Ar}$ ages ranging from 46.2 ± 0.4 Ma for a sample from the Middle Fork region of the basin to 33.0 ± 1.0

Ma for a sample from Commerce Creek in the North Fork region (Fig. 2) (Constenius, 1996; D. Archibald, written communication, 1997). Palynological analysis of a composite cuttings sample from the Cenex #4-13 Ladenburg well found a small number of late Paleocene-middle Eocene specimens in Kishenehn drill cuttings (Bujak Davies Group, written communication, 1989).

Strata of the Kishenehn Formation display a great variety of rock types, ranging from microlaminated oil shales and sapropelic coals to conglomerates and megabreccias (Price, 1965; Jones, 1969; McMechan and Price, 1980; Constenius, 1981; McMechan, 1981; Constenius and Dyni, 1983). Lithostratigraphically, the Kishenehn Formation has been divided into three parts, a Basal Member, a Lower Member, and an Upper Member. The contacts between these units are not exposed but are presumed to be conformable (Constenius, 1981; McMechan, 1981). However, in other western Montana basins discrete basin-fill sequences are bounded by regional unconformities (Fig. 3) (Robinson, 1960; Rasmussen, 1973; Fields et al., 1985; Hanneman and Wideman, 1991; Constenius, 1996). Additionally, Hanneman et al., (1994) observed that most sequence-bounding unconformities are marked by paleosols or paleosol stacks. Well-developed paleosols are exposed at only three localities in the North Fork region, Trail Creek, Coal Creek, and Camas Creek, in lower Kishenehn strata (Constenius, 1981). These paleosols may be evidence of a sequence boundary between middle Eocene strata of the Basal Member and late Eocene-Oligocene Lower Member strata. Aside from the potential sequence bounding, regional unconformity related, paleosols, the Kishenehn Formation has a demonstrable lack of mature paleosols and paleosol stacks that can be associated with long duration hiatuses in sedimentation. No angular unconformities or intrabasinal normal faults have been identified on reflection seismic profiles across the basin (Fig. 5). Furthermore, the angular unconformity reported by MacKenzie (1916) has been shown by McMechan and Price (1980) to be the product of sedimentary lensing and channeling. The lack of condensed sections (paleosols), unconformities and faults with major offset, within the Kishenehn sequence, combined with the affects of high sedimentation and subsidence rates, and the distribution of modern day exposures, allows us to make two important assertions: 1) widely strike-separated fossil localities along the Flathead River drainage are approximately the same age, Duchesnean-Chadronian (Figs. 2, 4); and, 2) there is relatively little geologic time represented at each cutbank-type exposure along the Flathead River and its tributaries.

The Basal Member in the North Fork region may be middle Eocene (Uintan) in age based on limited fossil data and, therefore, equivalent to Uintan strata of the Coal Creek and Pinchot members found in the Middle Fork region (Fig. 3). The Basal Member is a coarse-clastic, fluvial unit, consisting of yellow-tan and buff-colored conglomerate and conglomeratic sandstone with subordinate interbeds of carbonaceous mudstone and coal, that rests above erosionally truncated

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Fig. 5.—Seismic reflection profile S-S'. (See Figure 2 for location). Image processing includes migration to spatially restore reflections to their true position, time to depth conversion using velocity data from wells, and true-scale plotting (i.e., horizontal distance scale equals vertical depth scale). Notice that despite large-scale extensional movements on the Flathead fault (~10 km of displacement) that within the Kishenehn Formation layering is unbroken by normal faults (of significant size to be imaged on reflection seismic data) and there is no expression of intraformational angular unconformities. Seismic data courtesy of Explor Data Ltd., Calgary, Alberta, Canada.

Mesozoic, Paleozoic, and Precambrian rocks (McMechan, 1981; Constenius, 1981). Thickness estimates range from 140 m in British Columbia to 1,200 m in the west-central part of the basin in Montana (Fig. 4). In the Middle Fork region, middle Eocene rocks of the Kishenehn formation are a heterogeneous mixture of alluvial fan, fluvial, paludal, and lacustrine deposits that attain a composite thickness in excess of 1,500 m.

Overlying the Basal Member are the dominantly fine-grained fluvial-lacustrine strata of the Lower Member. These strata are discontinuously exposed along the North Fork of the Flathead and its tributaries and it is from this unit that most of our fossil collections have been obtained. Based on analysis of associated fossil vertebrates, invertebrates, and microflora, this unit is late Eocene (Duchesnean-Chadronian) in age. Significantly, even though we've established 15 fossil localities within the Lower Member, they are clustered in the middle of the basin and confined to a limited stratigraphic age-range (Figs. 2, 4). Strata assigned to the Lower Member are an intercalated assemblage of light gray and light gray-green siltstones, mudstones, lignites, oil shales, marlstones, sandstones, and conglomerates, and brick red and red-brown mudstones. The Lower Member attains a maximum thickness of about 2,000 m in Montana and more than 2,600 m in British Columbia (Jones, 1969:fig. 4).

Detailed sedimentologic study of the Lower Member in British Columbia by McMechan (1981) identified four main depositional environments of a low relief alluvial-floodplain system: 1) *braided river*, represented by a range of coarse clastic deposits from horizontally laminated-massive sandstones to lenticular bodies of conglomeratic sandstone and conglomerate, 2) *interfluvial*, characterized by massive to graded mudrocks, nodular marlstone, calcrete and gypsiferous mudstone, 3) *floodbasin pond and lake*, characterized by fossiliferous marlstone and siltstone, carbonaceous mudstone, microlaminated shale, lignite, carbonaceous sandstone and rare sandy conglomerate, and 4) *overbank near-channel floodplain*, comprised of calcareous claystone and mudstone, fossiliferous marlstone, coalified tree roots and stumps, and sandstone and pebbly conglomerate. Southward, in Montana, widening of the basin corresponds with an increase in lacustrine and paludal deposits in the lower part of the Lower Member, and with an increase in reddish-oxidized fan-delta and floodbasin deposits in the upper part of the unit (Constenius, 1981).

The Upper Member is a coarse-clastic unit composed of thick-bedded, boulder-cobble conglomerates, interbedded with sandstones, mudstones, and lignites. Paleocurrent, provenance, and other sedimentological data show that these are proximal alluvial fan and braided stream deposits derived from a rising mountainous terrain northeast of the Flathead Fault, the ancestral Clark and Livingston ranges (Price, 1965; Jones, 1969; McMechan, 1981). The presence of paleolandslide megabreccia deposits, that is, megaclasts of Cambrian and Devonian carbonates ranging from tens of meters to 1,800 m in length, provide evidence that there was significant paleotopographic relief across the Flathead Fault (Jones, 1969; McMechan, 1981). Dating of microfloral assemblages, a single vertebrate fossil (*Merycoidodon* sp.), and $^{40}\text{Ar}/^{39}\text{Ar}$ age of 33.0 ± 1.0 Ma establish an early Oligocene age for Upper Member deposits in British Columbia (McMechan, 1981; D. Archibald, written communication, 1997). Mammal fossils found in the Upper Member along Kintla Creek, Montana (Fig. 2) are early Oligocene-late Oligocene (Orellan-late Arikarean) suggesting that these are some of the youngest deposits

in the basin. The Upper Member is in excess of 2,100 m thick in British Columbia and is at least 1,500 m thick in Montana (Jones, 1969; Fig. 4).

The Kishenehn Formation is overlain along a pronounced angular unconformity by a thin veneer (0–100 m) of late Neogene alluvial gravels and glacial detritus. No middle Miocene to Pliocene deposits have been identified in the Kishenehn Basin. There is little evidence of Quaternary–Recent movement of the basin-bounding faults with the exception of the mountain-front fault and associated triangular facets at Nyack Flats. Quaternary glaciation may have removed evidence of late-stage extensional faulting and sedimentation, but these products of tectonism were not of the same magnitude as in southwest Montana, where late Miocene to Recent basin-fill is 100's to 1,000's of meters thick. Hence, subsequent to the middle Eocene–early Miocene episode of extension and sedimentation, the basin has been comparatively quiescent and was largely unaffected by Basin and Range extension (~17–0 Ma).

Methodology.—The North Kishenehn Basin is situated in rough, mountainous, heavily forested terrain. Roads are almost non-existent, being limited to a single, poorly maintained, gravel road originally linking Columbia Falls, Montana with Fernie, British Columbia along the west bank of the North Fork of the Flathead River. This road is now washed-out and abandoned in British Columbia. Since the road is currently impassable in British Columbia, access to the Canadian localities is now extremely difficult, requiring long, round-about approaches on narrow, heavily traveled logging roads. A second gravel road, in part nearly impassable, is east of the River in Glacier National Park. The latter terminates at Kintla Creek, some distance short of the international boundary. These roads provide limited point access to tributaries of the North Fork of the Flathead River at crossings. Access to the river itself is limited to those few places where the “main” road and the river approach and the terrain is suitable. Elsewhere, land access is very difficult due to rugged terrain, heavy vegetation, and few game trails. Climatic conditions for the area are typified by Polebridge, Montana (Fig. 2) in the south end of the North Kishenehn Basin. The reported mean annual temperature (MAT) is 3.7°C with January and July means of –8.5°C and 15.5°C. Annual precipitation is 57.2 cm, with more than half (57%) occurring principally as snow from October to March (www.worldwideweather.com).

The typical fossil locality is a cut bank along the Flathead River (Fig. 6), with a few localities on major tributaries, that exposes sediments of the Lower Member of the Kishenehn Formation. Most of these outcrops have to be approached by rafting the river. Due to often long distances between raft launching and landing points, visits to a given outcrop locality were necessarily brief, generally two to six hours on a given outcrop, and were of a reconnaissance nature, which permitted only small grab samples of obviously fossiliferous zones, with obvious specimens picked directly from outcrop. On rare occasions, a single outcrop locality would be subject to a near day-long visit in order to extract a significant mammalian specimen. Few localities were visited more than twice. In size, these outcrop localities varied from small, perhaps 3 m vertically above water level and perhaps 10–15 m in length, to quite large, over 30 m vertically and more than 100 m in length. Due to the near vertical nature of these cutbanks, collections were seldom made at heights greater than 3 or 4 m above water level. As a result, most localities were collected as a single unit without regard to local microstratigraphy. This appeared justified, since no evidence of significant faults or disconformity, other than the obvious unconformities between major units, e.g.,



Fig. 6.—Typical cutbank style exposure of Kishenehn Formation along the North Fork of the Flathead River. The senior author and Alan Tabrum are shown collecting invertebrate fossils at the Wurtz Bend fossil locality (NFF19). Photo by K. Constenius, September, 1991.

Basal and Lower members, and Upper Member to the overlying Quaternary till and alluvium, were noted at the various localities.

The fossiliferous sediments vary from silty shales and marls to fine, usually silty sandstones. Most molluscan fossils are badly crushed due to overburden compression. Disaggregation of the grab samples in water results in a hash of nearly unidentifiable fragments. Successful extraction of specimens requires stabilization upon exposure with a dilute solution of poly-vinyl acetate (PVA), then subsequent removal of additional matrix, softened by water, using dental tools and/or needle probes and additional PVA treatment. Most specimens required repeated steps to extract completely or to expose sufficiently for study. Some specimens were exposed only far enough to reveal significant characteristics, then, to avoid inadvertent breakage, left on small blocks of matrix.

SYSTEMATIC PALEONTOLOGY

Terrestrial Taxa

Order Archaeogastropoda Thiele, 1925
 Superfamily Helicinoidea Latreille, 1825
 Family Ceresidae Thompson, 1980

Type genus.—*Ceres* Gray, 1856.

Environment and Distribution.—The Ceresidae are known only from Mexico

and South America and contain five modern genera (Thompson, 1980:16–17). They are found in warm, moist, forested, tropical environments, often on a limestone substrate. The genus *Ceres* is endemic to eastern Mexico, in the states of Tamaulipas, San Luis Potosi, and Vera Cruz. Geologic range of the family is unclear. Other than genus *Tozerpina*, which ranges from Cretaceous to Oligocene in Alberta and Montana, I know of no other reference to this family as fossil.

Genus *Tozerpina* Bishop, 1980

Type species.—*Tozerpina rutherfordi* (Russell, 1929).

Discussion.—Although Bishop (1980:243, 245) clearly described the genus, and listed three included species, he did not designate a type species from among the three. *Tozerpina rutherfordi* is herein so designated, based on priority of publication of species, and as most typical of Bishop's Diagnosis of the Genus. The other two species included by Bishop are *T. douglasi* (Tozer, 1956) and *T. mokowanensis* (Tozer, 1956). The taxa following are hereby included and become the fourth, fifth, and sixth taxa of this genus, all fossil, extending the geologic range of the genus from latest Cretaceous into late(?) Eocene, and the size range down to 2.5 mm in width. Among the Ceresidae, which have great variety in apertural lamella, both in number and location, *Tozerpina*, with three lamellae, two palatal and one basal, appears most similar to the type genus, *Ceres*, which may also be keeled and the only modern genus in the family with palatal lamellae.

Tozerpina buttsi (Russell, 1956), **new combination** (Fig. 7.A–7.C)

Triodopsis buttsi Russell, 1956a:108, 109, figure 3, plate I, figures 1–6; 1964:538, 541; Ross, 1959: 70, 71; Roth, 1986:table 2; Constenius et al., 1989:table 2.

Discussion.—Russell's (1956:108, 109, fig. 3, pl.1, figs. 1–6) type specimens were examined to determine that this species rightfully belongs to the genus *Tozerpina* as defined by Bishop (1980:243, 245). They differed from the type description only in possessing a peripheral keel. Russell (1956:109) reported "*Triodopsis*" *buttsi* from only one locality, his E-4. His exact locality has been subsequently destroyed by erosion and construction of a highway bridge. Although there are molluscan bearing sediments at the approximate locality, no identifiable *Tozerpina* were among the taxa recovered there, although fragments recovered may represent one or more species of the genus. Figures 7.A–7.C are of Russell's holotype (1956:106), Geological Survey of Canada (GSC) 11606, diameter 4.5 mm, height (crushed, estimated) 2.25 mm, 5 whorls.

Tozerpina buttsi parva Pierce, **new subspecies** (Fig. 7.D–7.I)

Diagnosis.—A small *Tozerpina buttsi*, nearly identical in all proportions, but with slightly stronger and more closely spaced collabral costellae.

Description.—Shell tiny, lenticular, of about 4.50 to 4.75 whorls, inner walls of initial whorls resorbed, periphery modestly carinate, suture scarcely impressed. Embryonic whorls about 1.5, finely granulose, later whorls with fine, very closely spaced collabral costellae, about 20 per circumferential millimeter, initially faint, becoming stronger on later whorls, costellae continue over periphery, becoming somewhat weaker, but continue to margin of a large callus pad ($\frac{1}{2}$ diameter) that conceals the umbilicus. Aperture ovate-lunate, retractive at about 45°, with three teeth, outer lip strongly thickened and reflected, slightly sinuous above periphery, edge rebated by rounded groove extending from suture to umbilicus. Upper palatal tooth located midway between periphery and upper insertion, initially wide

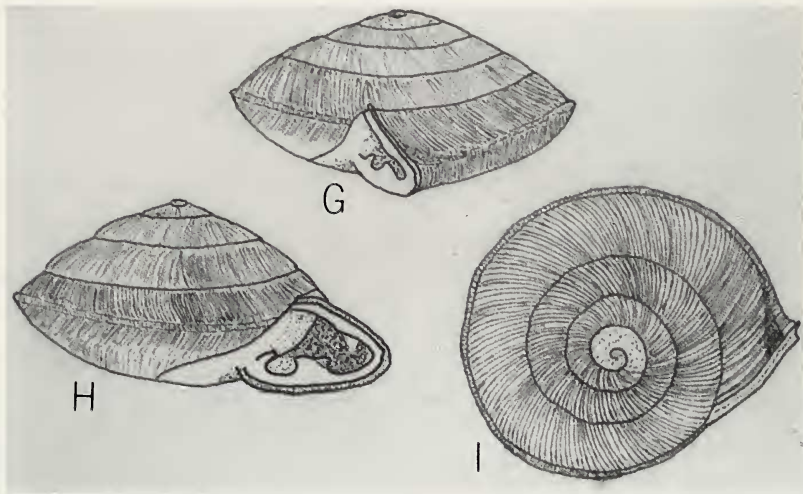
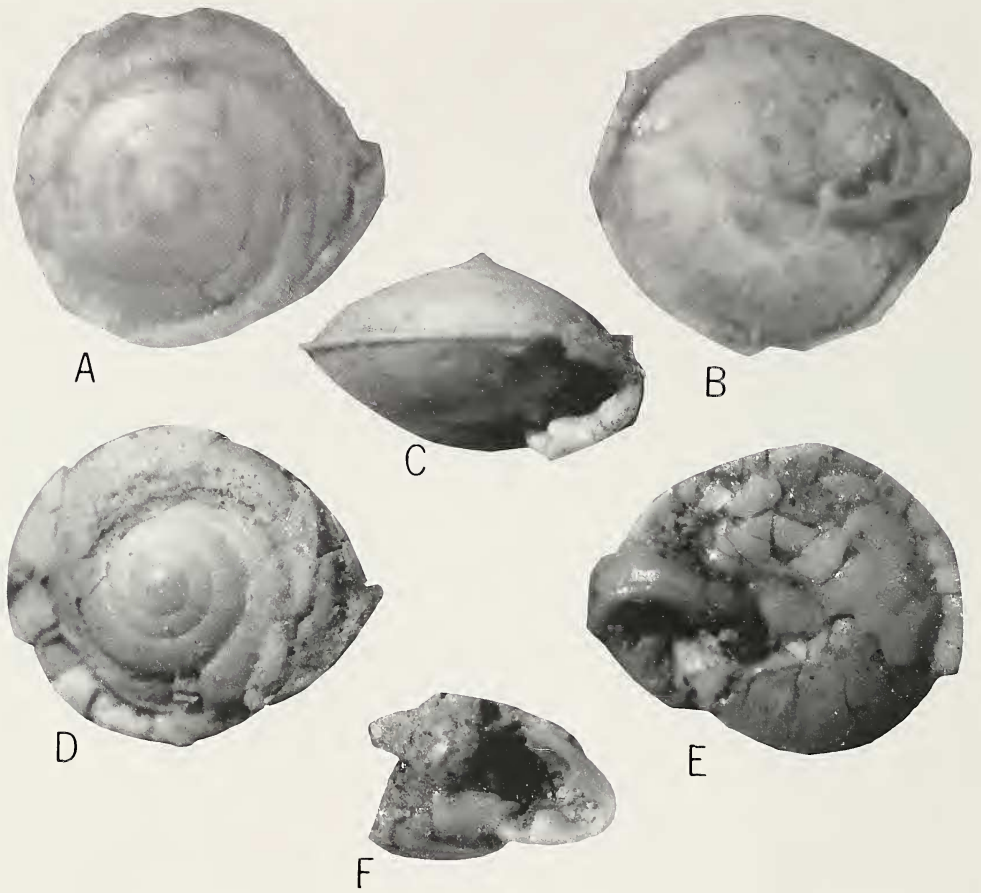


Fig. 7.—ARCHAEGASTROPODA: CERESIDAE. A–C: *Tozerpina buttsi* (Russell, 1956), Holotype (GSC 11606), X10; A. apical; B. umbilical; C. apertural; D–F: *Tozerpina buttsi parva* n. ssp., X16; D–E. Holotype (CM 41614); D. dorsal; E. umbilical; F. Paratype (KUMIP 289700), aperture; G–I: reconstruction X16; G. lateral; H. apertural; I. dorsal.

and blunt, becoming narrower and sharply crested, deeply entering, slanting downward, causing descending, deeply impressed dorsal sinus on exterior of shell behind lip, the outer margin of which rises to become the peripheral carina. Lower palatal tooth located about midway between periphery and columella, narrower and higher, spirally entering, crest deflected adaxially with rounded groove below crest, may develop secondary node on abaxial side shortly after entering, forms short, shallow sulcus below and behind the lip, palatal teeth form prominent oval sulcus on inside of peripheral margin of lip, which merges with the descending, sharply rounded ridge of the dorsal plica shortly behind lip. Basal tooth very close to columella, fine, shorter, crest deflected abaxially, spirally entering, separated from lower palatal tooth by small, rounded sulcus. Parietal callus strong, margin curved, joining with heavy basal callus. Measurements of holotype: width, major 2.5 mm; minor 2.3 mm; height 1.45 mm; H/W 0.58; about 4.5 whorls. Ranges: width, major 2.5 to 3.0 mm; minor 2.3 to 2.75 mm; height 1.45 to 1.55 mm, most crushed; 4.5 to 4.75 whorls.

Discussion.—*Tozerpina buttsi parva* is, quite simply, a miniature *T. buttsi*, proportionally smaller in all measurements, and is not simply a less mature specimen. *Tozerpina buttsi buttsi*, at 4.5 to 4.75 whorls, typical of mature *T. buttsi parva*, is still much larger in all dimensions. *Tozerpina buttsi parva* also differs from the nominate form in having slightly stronger, and more closely spaced, collabral costellae. *Tozerpina lentis*, described subsequently herein, differs from *T. buttsi parva* in being much larger, lacking a peripheral carina, and having coarser costellate. *Tozerpina buttsi parva* is, by far, the smallest species of its genus and one of the smallest of its family.

Tozerpina rutherfordi (Russell 1929) differs from *T. buttsi parva* in being much larger, width 9 mm, in having two parietal lamellae, a deep set palatal lamellae beginning well behind the lip, and six costellae per millimeter on the ultimate whorl. *Tozerpina douglasi* (Tozer, 1956) also differs in size, 10 mm, and in having spiral as well as radial sculpture with 15 radial costellae per millimeter on the ultimate whorl. The Cretaceous species, *T. mokowanensis* (Tozer, 1956), width of 5 mm, has 20 costellae per millimeter on the ultimate whorl, and a keeled periphery, and most closely approximates *T. buttsi parva*. It, too, is larger, and differs in having only one palatal lamella, and a body whorl that descends slightly in the last millimeter. *Tozerpina buttsi* and *T. mokowanensis* are the only species of this genus with a keeled periphery.

Etymology.—Latin *parva*, small or little.

Material.—More than 30 specimens. Holotype CM 41614, and paratypes CM 41615 (2), KUMIP 289,700, KUMIP 289,701 (2), PCER-104 (10 fragments), and PCER-105 (2 molds w/plastitypes) are from Commerce Creek (CMC-1) locality, British Columbia. Paratypes: PCER-101 (2), PCER-102 (10 fragments), PCER-103, and PCER-106 (2) are from E-5 (NFF-1) locality, British Columbia. All specimens from the Lower Member, Kishenehn Formation, late Eocene.

Tozerpina lentis Pierce, **new species** (Fig. 8.A–8.E)

Diagnosis.—A small, lenticular *Tozerpina* of about five whorls, with about six collabral costae per circumferential millimeter at periphery of the last whorl, and a heavily strengthened retractive aperture containing three teeth.

Description.—Shell small, lenticular, 4.75 to 5.25 whorls, inner walls of initial whorls resorbed, periphery roundly acute but not keeled, suture scarcely impressed. Embryonic whorls about 1.75, finely granulose, later whorls with about six regular collabral costae per circumferential millimeter, initially weak, becoming very distinct on later whorls, weakening slightly after passing over periphery, but continuing until covered by large callus pad that conceals umbilicus. Aperture ovate-lunate, retractive at about 45°, outer lip strongly thickened and reflected. Teeth three, upper palatal tooth located nearer insertion, initially blunt, deeply entering, becoming narrower and more sharply crested, curving slightly abaxially, causing impressed sulcus on upper lip, lower palatal tooth located midway between periphery and insertion, narrower and higher, entering spirally, crest deflected adaxially, basal tooth

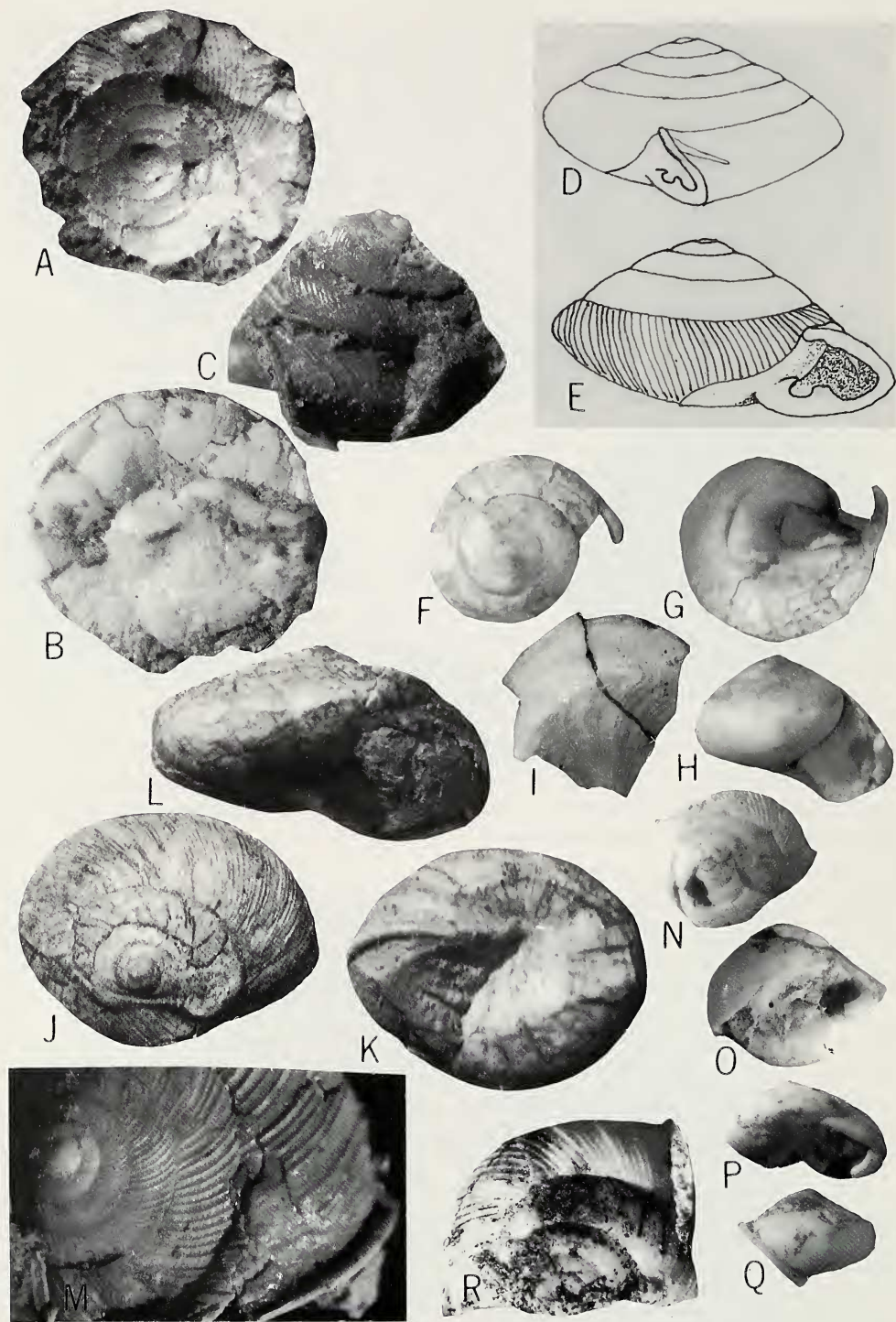


Fig. 8.—ARCHAEGASTROPODA: CERESIDAE. A–E: *Tozerpina lentis* n. sp., X10; A–B: Holotype (CM41616); A, apical; B, umbilical; C, Paratype (CM 41617), X10, lateral, laterally compressed; D–

small, very close to columella, crest deflected abaxially, spirally entering, separated from lower palatal tooth by rounded sulcus. Parietal callus thick, margin curved to join thick basal callus. Measurements of holotype: width, major 4.6 mm; width, minor 4.0 mm; height about 2.5 mm, crushed; 5 whorls. Ranges: width, major 4.0 to 4.8 mm; width, minor, 3.5 to 4.4 mm; height, ?, all specimens crushed; whorls 4.5 to 5.25.

Discussion.—*Tozerpina lentis* most resembles *T. buttsi buttsi*, but, although of about the same size, it differs in having a coarser sculpture (~six costae versus 15–20 costellae per mm), an acutely rounded periphery, and in the position of the upper palatal tooth and the associated external sulcus behind the outer lip. Among the older Cretaceous-Paleocene taxa of the genus, it shares the characteristic of three palatal lamellae with *T. douglasi* and of six costae per mm with *T. rutherfordi*, but differs from the former in size, and in lacking spiral sculpture, and from the latter in size and in lacking parietal lamellae. Fragments found at Locality E-5 (NFF-1) may represent *T. lentis*.

Etymology.—Latin *lentis*, lentil, lens-shaped.

Material.—Nine specimens. Holotype CM-41616, and paratypes CM-41617 (2), KUMIP 289,702 (2), PCER-107 (2), and PCER-108, are from Kintla Creek/River (NFF-17) locality, Flathead County, Montana, eight specimens. Type horizon: Lower Member, Kishenehn Formation, late Eocene. PCER-109 is from E-5 (NFF-1) locality, British Columbia, Lower Member, Kishenehn Formation, late Eocene.

Family Helicinidae Latreille, 1825

Type genus.—*Helicina* Lamarck, 1799.

Subfamily Hendersoninae Baker, 1926

Type genus.—*Hendersonia* A. J. Wagner, 1905.

Environment and Distribution.—Recent *Hendersonia* are “found on well-shaded, leafy, and rather humid slopes, on limestone terranes” and are spottily distributed “in the upper Mississippi Valley east to the Alleghenies in Pennsylvania and North Carolina” (LaRocque, 1970:555–556). Recent *Waldemaria* live only in Japan, although it is known as fossil from middle Miocene (early Barstovian) Flint Creek beds of southwestern Montana (Pierce and Rasmussen, 1989), where there is a suggestion of a moist, temperate climate.

Genus Waldemaria Wagner, 1905

Type species.—*Tomichia japonica* (Adams, 1861:308).

Waldemaria monticula Pierce, 1989

(Fig. 8.F–8.I)

Discussion.—Except for minor differences such as the body whorl being slightly more rounded than the holotype, which could easily fall within the range of normal specific variation, and the presence of low obscure costae (about six per circumferential millimeter) overprinted on the fine collabral costellae (>20 per

←

E: restoration; D: lateral; E: apertural; HELICINIDAE. F–I: *Waldemaria monticula* Pierce, 1989 (in Pierce and Rasmussen, 1989), F–H: Hypotype (CM 41622), X5; F: dorsal; G: umbilical; H: apertural; I: *W. monticula*, Hypotype (PHCN 117), X10, partial operculum; J–M: *Lucidella columbiana* n. sp., J–L: Holotype (CM 41620), X5; J: apical; K: umbilical; L: apertural; M: *L. columbiana* Paratype (KUMIP 289705) X10, apical detail, apex to lip; N–R: *Lucidella salishora* n. sp., N–Q: Holotype (CM 41618), X5; N: apical; O: umbilical; P: apertural; Q: lateral; R: *L. salishora*, Paratype (KUMIP 289704), X10, apical detail, apex to lip.

millimeter) on the last two whorls, which may have been worn off the holotype, there are no significant differences between these specimens and the holotype. A partial *Waldemaria*, cf., *W. monticola* operculum was recovered at locality CMC-1 (Figure 8.I) although not in direct association with the single crushed specimen from that location. This operculum, although incomplete, compares almost perfectly with the operculum of the holotype (Pierce and Rasmussen, 1989:fig. 2-2, 2-5). There is no hesitation in identifying these specimens as *W. monticola*. Measurements of hypotype: width, major 9.2 mm; width, minor 8.5 mm; height 8.0 mm; H/W 0.87; 4.75 whorls.

Material.—Ten specimens. Figured specimen CM-41622 and hypotypes CM-41623, PHCN-114 (2) are from Lower Kintla Rapids (NFF-18) locality. Additional hypotypes: KUMIP 289,707 is from Wurtz Bend (NFF-19) locality; PHCN-115 (3) is from E-4 (NFF-2) locality; PHCN-116 is from Commerce Creek (CMC-1) locality (1), both British Columbia, all from Lower Member, Kishenehn Formation, late Eocene. A partial operculum of *Waldemaria*, cf. *W. monticola*, PHCN-117 was recovered at the Commerce Creek (CMC-1) locality, British Columbia, same horizon.

Subfamily Helicininae Latreille, 1825

Type genus.—*Helicina* Lamarck, 1799.

Genus *Lucidella* Swainson, 1840

Type species.—*Helix aureola* Férussac, 1822.

Subgenus *Poeniella* H. B. Baker, 1923

Type species.—*Helicina (Plicatula) christophori* Pilsbry, 1897 (*vide* Pilsbry, 1948:1085).

Discussion.—The subgenus *Poeniella* is distinguished by axial riblets with or without spiral striae.

Environment and Distribution.—The genus *Lucidella* is found in warm, moist tropical environments, usually well wooded, and is found throughout the Greater and Lesser Antilles, and circum-Caribbean from Venezuela to Yucatan (Thiele, 1992:127), and southern Vera Cruz (Baker, 1922:36). Although the subgenus *Poeniella* is most diverse on Hispaniola (Pilsbry, 1928:479), there are several species on Cuba (Aguayo y Jaume, 1947–1951:395), one of which has also been found in the Florida Keys (Pilsbry, 1949:1085). Geologic range of the subgenus is unknown. Pre-Quaternary fossils of the genus *Lucidella* are almost unknown. I have examined the type material for "*Helicina*" *oregona* Hanna 1920, from the Oligocene John Day beds of Oregon, and find that it is, unquestionably, a *Lucidella*, intermediate in size between the two new species described herein. Goodfriend and Mitterer (1988:301) reported two extant species as latest Pleistocene fossils from Jamaica.

Lucidella columbiana Pierce, **new species**

(Fig. 8.J–8.M)

Diagnosis.—A large *Poeniella* with sinuous collabral costae crossing microscopically faint spiral costellae, noticeably constricted behind dorsal margin of outer lip, aperture reflected and reinforced but without teeth.

Description.—Shell large, depressed conic globose, whorls 4.75, umbilicus covered by callus pad, inner partitions of spire resorbed, sutures scarcely impressed. Embryonic whorls about one, very finely and irregularly punctate, nucleus 0.45 millimeter in diameter, subsequent two whorls finely and faintly costellate, costellae collabral, slightly sinuous, superimposed on very faint spiral costellae that weaken on ultimate whorls, but still visible under high magnification, especially on base, last 1.75 whorls costate, about seven per circumferential millimeter, continue over rounded periphery only slightly

diminished until covered by umbilical callus. Aperture lunate-ovate descending in last millimeter, retractive from axis about 45°, outer lip reflected and reinforced moderately, narrowly constricted behind dorsal margin of outer lip, parietal callus extends to smooth to finely granulose callus pad hiding umbilicus, umbilical callus about $\frac{1}{2}$ diameter of shell. Measurements of holotype: width, major, 9.4 mm; width, minor, 9.0 mm; height 5.2 mm; whorls 4.75; H/W 0.55.

Discussion.—*Lucidella columbiana* resembles both “*Helicina*” *oregona* and *Lucidella salishora*. “*Helicina*” *oregona* is smaller, has more whorls, 6 versus 4.75, taller, H/W 0.625 versus 0.55, is more finely costate, 9–10 versus 7 per millimeter, with the costae fading nearly completely on the base, and it has a basal tooth in the more prominently descending aperture. *Lucidella columbiana* appears to be most similar to *L. salishora*, which differs in having more whorls with angular juvenile whorls, being much smaller, having a strong thickening of the upper portion of the outer lip, and a narrow, deep constriction behind the entire outer lip.

Etymology.—Named with reference to the Columbia River, of which the Flathead River is a tributary.

Material.—Fifteen specimens. Holotype, CM-41620, and paratypes: CM-41621 (2); KUMIP 289,705; KUMIP 289,706 (2); PHCN-110; and PHCN-111 are from E-5 (NFF-1) locality, British Columbia, Lower Member of the Kishenehn Formation, late Eocene. Additional specimens: Commerce Creek (CMC-1) locality, PHCN-1143(6); locality data as above, and Wurtz Bend (NFF-19) locality, PHCN-112, Flathead County, Montana, both localities in Lower Member, Kishenehn Formation, late Eocene.

Lucidella salishora Pierce, new species

(Fig. 8.N–8.R)

Diagnosis.—A moderately large *Poeniella* with sinuous collabral costae crossing microscopically faint spiral costellae, noticeably constricted behind outer lip, which is strongly thickened on dorsal margin, without basal tooth.

Description.—Shell of moderate size, conic globose, whorls 5.25–5.50, inner partitions of spire resorbed, sutures scarcely impressed. Embryonic whorls about 1.25, finely punctate, nucleus 0.3 mm in diameter, neanic whorls about 0.75 with very fine collabral costellae, which become prominent and more widely spaced sinuous collabral costae, about six per circumferential millimeter, on last three whorls, continue over roundly angular periphery, diminishing somewhat on base, crossing faint spiral costellae until covered by callus. Initial four whorls distinctly angular at periphery. Aperture roundly lunate externally, descending slightly in last millimeter, very noticeable narrow constriction immediately behind outer lip, outer lip reflected and roundly thickened to an acute margin, retractive from axis almost 60°, interior margin of upper part of outer lip has wide, low, blunt reinforcement over $\frac{2}{3}$ of distance from point of insertion to periphery, about twice as thick as remainder of lip when viewed aperturally, giving inner margin of aperture a roundly angular shape. Base slightly sunken, covered by smooth to faintly granulose callus pad that merges with parietal callus. Measurements of holotype: width, major, 5.0 mm; width, minor, 4.2 mm; height 2.5 mm; H/W 0.5; whorls 5.25. Measurement of aperture: width 1.2 mm, height 1.7 mm. Range of measurements: width, major, 3.6–5.7 mm; width minor, 3.0–4.6 mm; height, 2.3–3.3 mm; H/W 0.50–0.64; whorls, 5.25–5.50.

Discussion.—The “axial, instead of spiral riblets” (Baker, 1923, 9.23) clearly place *Lucidella salishora* in the subgenus *Poeniella*. It rather closely resembles modern Cuban *Lucidella rugosa* (Pfeiffer, 1839) and Cuban and Floridian *Lucidella tantilla* (Pilsbry, 1902), having similar sculpture, H/W ratios, and in lacking a basal tooth. It differs from the aforementioned primarily in size and in the coarseness of the sinuous collabral costellae. The Oligocene “*Helicina*” *oregona* is similar in size and is noticeably constricted behind the aperture, especially dorsally. It differs from *L. salishora* in being slightly larger, taller, H/W 0.62 versus 0.50, more finely costate, 9–10 versus six per millimeter, has an aperture

that descends more noticeably, lacks the thickening of the dorsal portion of the outer lip, and has a blunt basal tooth separated from the columella by a rather deep notch.

Etymology.—Named to honor the Salish speaking Flathead Indians.

Material.—More than 150 specimens. Holotype, CM-41618, and paratypes: CM-41619 (3); KUMIP 289,703; KUMIP 289,704 (3); PHCN-103-106 (63), PHCN-109 (10) are all from Commerce Creek (CMC-1) locality, British Columbia (>100 specimens). Type horizon is the Lower Member, Kishenehn Formation, late Eocene. Additional localities are as follows: E-5 (NFF-1), PHCN-107 (23), and E-4 (NFF-2), PHCN-108 (15), both British Columbia, horizon as above.

Order Stylommatophora Schmidt, 1835

Superfamily Succineoidea Beck, 1837

Family Succineidae Beck, 1837

Type genus.—*Succinea* Draparnaud, 1801.

Genus *Oxyloma* Westerlund, 1885

Type species.—*Succinea dunkeri* Pfeiffer, 1849.

Oxyloma? kintlana Pierce, **new species**

(Fig. 9.A)

Diagnosis.—Shell narrow with long acute spire, and narrowly ovate-lunate aperture about as tall as the spire.

Description.—Shell narrow, of more than three rounded, expanding whorls, suture well impressed, spire long, acute, nucleus of embryonic whorls elevated, acute, very finely costulate, remaining whorls with sculpture of fine, closely packed, orthocline growth wrinkles. Aperture narrowly ovate-lunate, about equal to spire height, peristome simple, sharp. Measurements of figured holotype, CM 41628: height (est.), >8 mm; width (est.), 4 mm; height of aperture, 4 mm; whorls (est.), >3.

Discussion.—All specimens are badly crushed and incomplete, but all features except the columella can be seen on one or more of the specimens. Under the best of circumstances, it is next to impossible to identify succineids from shell alone, except for the genus *Oxyloma*. The condition of the specimens at hand precludes precise identification of even that genus. Overall character of this species does, however, strongly suggest that these specimens are, indeed, *Oxyloma* and, most probably, in the *O. effusa* Group (Section *Neoxyloma* Pilsbry) (Pilsbry, 1948:777). This species is very different from late Oligocene (Succineidae) *montana* Pierce, 1992, and all other succineids reported from pre-Pliocene strata (Galbreath, 1969:91–94, fig. 1d; White, 1883:45,46, pl. 19, fig. 4a).

Etymology.—*kintlana*, with reference to the type location along Kintla Creek, a west flowing stream entering the Flathead River from Glacier National Park, Montana.

Environment and Distribution.—The *O. effusa* Group is North American, generally north of the 35th parallel, but extends into Florida, and is essentially absent from the Southwest and Far West of the U. S. They are normally encountered in well-vegetated, permanently marshy to swampy localities (LaRocque, 1970:697–699). Geologic range of the succineids is not well understood, partially due to the fragile nature of the shell, and to the intergrading shell morphology among species, but is probably of great antiquity, based on their anatomy (Patterson, 1971). The genus *Oxyloma* is fairly common in late Pliocene (Blancan) faunas on the High Plains. The late Oligocene (Succineidae) *montana* Pierce, 1992 may be a *Catinella*. Galbreath (1969) found what could well be succineids in the Oligo-Miocene of northeastern Colorado, but, being molds, precise identification is not

possible. Eocene "*Succinea*" *papillispira* White, 1876, may not be a succineid (Pierce, 1992:611).

Material.—Four specimens. Holotype and figured specimen, CM-41628 and paratypes CM 41629 (3), are from Kintla Creek River (NFF-17) locality, Flathead County, Montana. Two unidentifiable succineid spire fragments from South Ford Creek (NFF-22) locality, PSUC-105, may represent this species. All localities in Flathead County, Montana, Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Genus *Omalonyx* Orbigny, 1841

Type species.—*Succinea unguis* Martens, 1873:193.

Discussion.—This is a slug-like genus of the Succineinae (*s. str.*) that currently inhabits Central and South America and the Antilles. Thiele (1992:800–801, figure 587), using an alternative spelling of *Homalonyx*, describes the genus as: "Shell flatly bulging, fingernail shaped, with very small terminal spire and very wide, elongated oval aperture, covered by the mantle along the margin or completely." Patterson (1971:147–151; 181; 187; 193–195, figures 38–46) has studied *O. felina* Guppy, 1872, and amplifies the shell description as follows: "The shell of the largest individual measures 11.5 mm in length 7.3 mm in width with an aperture length of 11 mm (Fig. 38). The shell is very depressed in side view and has one $\frac{1}{4}$ whorls. There is no spire. The aperture occupies almost the entire shell, and is oval in shape. There is no columellar plait but there is a noticeable columellar flange which projects into the aperture. The shell is very thin, transparent and light amber in color. The coloration is slightly darker at the apex. The shell is sculptured with fine, readily visible growth lines and some widely spaced radial lines which can be seen only with transmitted light. The shell has a glossy appearance inside and out. The edge of the mantle encircles the peripheral 2 mm of the shell."

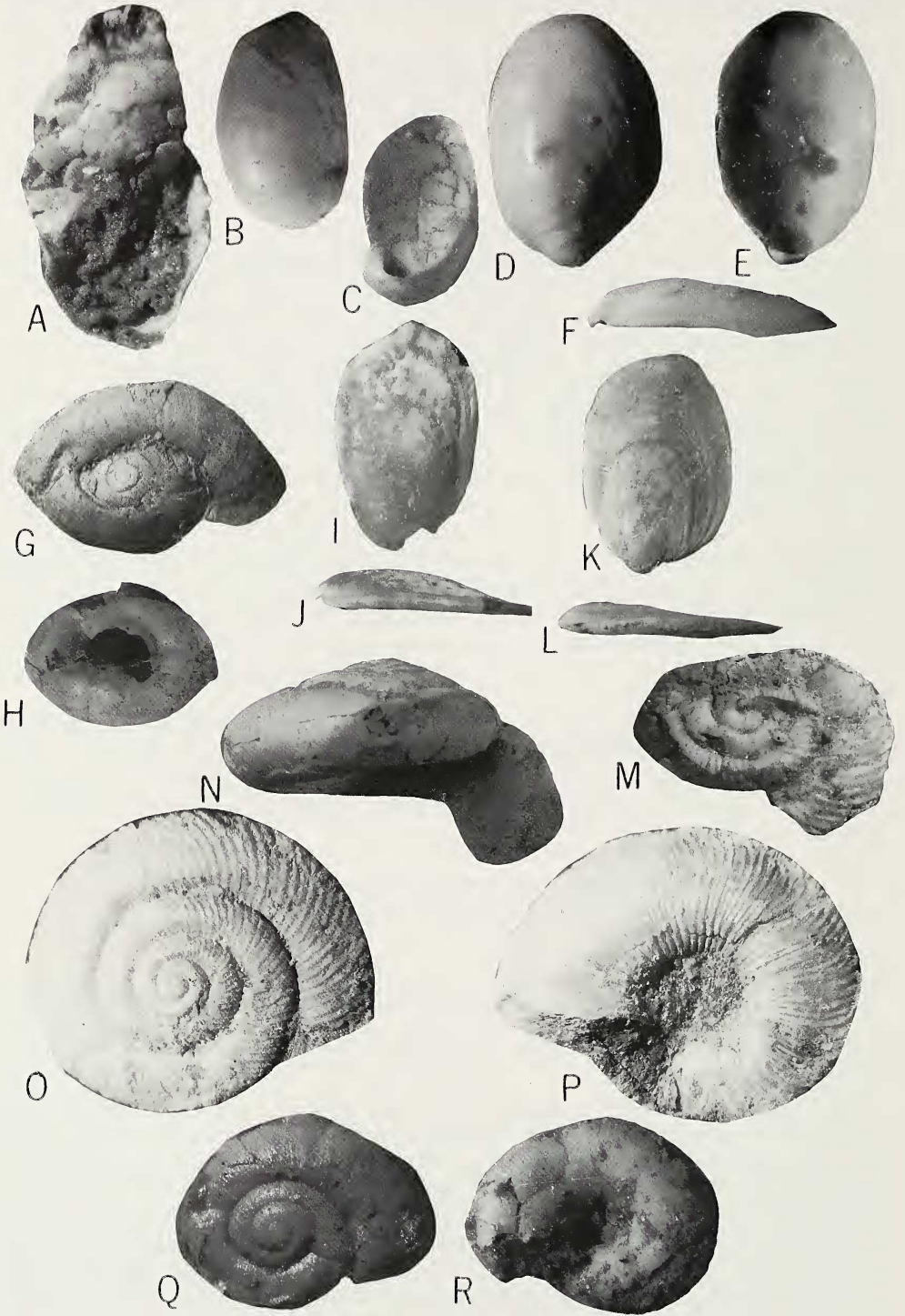
Environment and Distribution.—"Omalonyx is a slug-like succineid inhabiting tropical Central and South America and various islands of the West Indies. There are only a few recognized species and all are amphibious in habit, living near or on emerging vegetation of bodies of freshwater" (Patterson 1971:181). Geologic range is unknown.

Omalonyx antiqua (Russell, 1956a), **new combination** (Fig. 9.B, 9.C)

Binneya antiqua Russell:1956a, p. 112–113, fig. 7, pl. 3, figs. 7–10

Description.—"Shell small, oval, low, consisting of about one whorl which expands rapidly to form a broad, shallow body cavity, with the posterior margin somewhat turned in ventrally as part of a vestigial spire. Outline more convex on left side than on right. Surface almost smooth, with occasional faint growth lines. Length of holotype, 5.7 mm; width 3.8 mm" (Russell, 1956a:112–113).

Discussion.—It has been recognized for some time that there is a serious problem with the taxonomic position of "*Binneya*" *antiqua* Russell, 1956a. Roth (personal communication, 1990) early recognized that assigning this species to the genus *Binneya* Cooper, 1863 was inappropriate. Comparison with specimens of *Binneya notabilis* Cooper, 1863, kindly provided by Roth, quickly confirmed this. The shape of the shell provided strong evidence that the animal had been slug-like, but attempts to fit "*B.*" *antiqua* into the other slug-like families were less than satisfactory. The Limacidae provided a possible fit, but it, too, was far from satisfying. The hard, calcitic shell of "*B.*" *antiqua*, originating from a spire



of 0.25 to 0.50 whorl, differs markedly from the normal character of limacid slug plates (shells). The shell of "*B.*" *antiqua* does compare well with the descriptions of the genus *Omalonyx* in almost all ways. The only difference noted is the shell is slightly thicker than described for *O. felina*. The net result is to remove "*B.*" *antiqua* from the genus *Binneya* and place it within the succineid genus *Omalonyx*, a much more satisfactory taxonomic position.

Omalonyx cocleare Pierce, **new species**
(Fig. 9.D–9.F)

Diagnosis.—A small, spoon-shaped shell, embryonic shell with 0.25 to 0.50 dextral whorls before elongate aperture nearly as tall as shell.

Description.—Shell small, substantial, elongate, gently rounded, inverted spoon shaped, convex up, with smooth, shiny, solid, white dorsal inductura, basal concavity (aperture) nearly as large as shell, containing yellow, crystalline calcite inner layer, partially to nearly filling the concavity; embryonic shell begins with about 0.25 to 0.50 dextral whorls before opening into an elongated, ventrally located, aperture, subsequent growth elongate and widening to attain an oval, spoon shape with a bluntly rounded distal margin, protoconch smooth, slightly protruding from posterior margin of shell with apex well curved to right, distinct hook shape ventrally; convex dorsal surface of shell sculptured with weak, closely spaced, semicircular growth costellae, with one or more costellae somewhat stronger. Measurements of holotype, CM 41630: height (length) 3.8 mm; width 2.2 mm; thickness 0.7 mm; whorls about 0.35.

Discussion.—This taxon was first thought to be a form of *Omalonyx antiqua*, which Russell (1956:112–113, pl. 3, figs. 7–10) had collected from his nearby locality E-4. Subsequent evaluation under the microscope showed this taxon to be distinctly different, with less than 0.50 whorl coiling in the embryonic stage before growth becomes linear. In *O. antiqua*, the initial spiral stage lasts one, or slightly more, whorls. It should be noted that, despite careful collection of our E-4 locality, no specimens of *O. antiqua* were recovered. However, the locality collected as E-4 was not, in fact, exactly the same as Russell's early 1950's locality. Flood erosion, and construction of a modern highway bridge, have severely modified the local terrain. All other taxa listed by Russell (1956:105) from his Locality E-4, except *Tozerpina buttsi* (*Triodopsis buttsi*) (Russell, 1952), were collected.

Comparison with *Deroceras pachyostrakon* (Taylor, 1954) from the Pliocene of California, which also has a short initial spiral stage of about 0.1 whorl, showed major differences in the character of the inductura. The inductura is hard, dense, relatively thick and shiny for *O. cocleare*, versus chalky, thin and dull for *D. pachyostrakon*, which also has a much thicker inner yellow calcitic layer.

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Fig. 9.—STYLOMMATOPHORA: SUCCINEIDAE. A: *Oxyloma? kintlaense* n. sp. holotype (CM 41628), X5, apertural; B–C: *Omalonyx antiqua* (Russell, 1956) Holotype (GSC 11621), X5; B. dorsal; C. ventral; D–F: *Omalonyx cocleare* n. sp. Holotype (CM 41630), X10; D. dorsal; E. ventral; F. lateral; HAPLOTREMATIDAE. G–H: *Haplotrema simplex* (Russell, 1956) X3; G. Hypotype (CM 41653), apical; H. Hypotype (PHPL-102) umbilical. LIMACIDAE. I–J: *Deroceras securis* Pierce, 1992 Hypotype (CM41663), X5; I. dorsal; J. lateral; K–L: *Deroceras mahiz* Pierce, 1992 Hypotype (CM 41665), X5; K. dorsal; L. lateral. DISCIDAE. M. *Discus mackenziei* Russell, 1956 Hypotype (KUMIP 289733), X10; N–P: *Anguispira* sp., c.f. *A. alternata* (Say, 1816); N. Hypotype (CM 41661), X3, apertural; O–P: Hypotype (KUMIP 289734), X5; O. apical; P. umbilical. ZONITIDAE. Q–R: *Nesovitrea pulchra* Pierce, 1992 Hypotype (CM 41667), X10; Q. apical; R. umbilical.

Etymology.—*cocleare*, Latin, a spoon, a reference to the shape of the shell.

Material.—Twenty specimens. Holotype, CM-41630, and paratypes: CM-41631 (3); KUMIP 289,710; KUMIP 289,711 (3); PSUC-106 (2), and PSUC-107 (5) are from Commerce Creek (CMC-1) locality; additional paratype PSUC-108 (5) is from E-5 (NFF-1) locality, both British Columbia, Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Superfamily Pupilloidea Turton, 1831

Family Pupillidae Turton, 1831

Subfamily Pupillinae Turton, 1831

Genus *Pupoides* Pfeiffer, 1854

Type species.—*Bulimus nitidulus* Pfeiffer, 1839, by subsequent designation (Kobelt, 1880).

Subgenus *Ischnopupoides* Pilsbry, 1926

Type species.—*Pupa hordacea* Gabb, 1866.

Environment and Distribution.—Characteristic of dry country, essentially the Rocky Mountain states of western United States, from southwest South Dakota through Arizona to the state of Sinaloa, Mexico, with an outlying species in western South America (Pilsbry, 1948:924; Bequaert and Miller, 1973:58–59). *Pupoides hordaceus*, which is similar to the following species, is a dry country species, generally inhabiting the Upper Sonoran Life Zone of the southern Rocky Mountains, from southeastern Wyoming to New Mexico and all of Arizona but not, apparently, found in adjacent Sonora, Mexico (Bequaert and Miller, 1973: 58–59, 177). Known geologic range of *Ischnopupoides* is from late Eocene-early Oligocene (Chadronian) (*P. tephrodes* Roth, 1986:245–247), and late Oligocene (Arikareean) (*P. montana* Pierce, 1992), through the Quaternary.

Pupoides costatus Pierce, **new species**
(Fig. 10.A–10.C)

Diagnosis.—A small cylindrical *Ischnopupoides*, whorls short, sculptured with bold, regularly and widely spaced prosocline riblets, which are separated by two to five very fine costellae between each riblet on last whorls, and with a modestly everted, slightly thickened peristome.

Description.—Shell dextral, of about 5.25 short whorls, very narrowly rimate, cylindrical to slightly pupilliform with convex low conic apex, suture moderately impressed, and appearing crenulated by the riblets on later whorls. Nuclear whorls 1.5, smooth to finely punctate, neanic whorls initially with slender, regularly spaced prosocline costellae becoming more widely spaced riblets on later whorls, riblets spaced about six per mm on penultimate whorl and three to four per mm on body whorl, riblets separated by two to five (usually three) faint parallel costellae on last several whorls. Body whorl ascends moderately in last quarter whorl, slightly compressed laterally resulting in a weakly rounded keel, regaining a “U” shape at the prosoclinally oblique (~20°) aperture, peristome everted modestly, thickened within, thin callus on parietal margin, no tubercles or teeth. Dimensions of holotype: height 3.1 mm; diameter (estimated*) 1.5 mm; H/D 2.06; whorls 5.25. *—Shell laterally compressed, average of measurements with compression (1.9 mm) and normal to compression (1.1 mm).

Discussion.—Both riblets and costellae appear slightly less prominent on specimens from the type locality than from the Canadian localities. There is little difficulty in placing *Pupoides costatus* in the subgenus *Ischnopupoides*. *Pupoides costatus* is quite similar to both early Oligocene *Pupoides tephrodes* Roth, 1986 from the Three Forks Basin of Central Montana and to late Oligocene *Pupoides montana* Pierce, 1992 from the Deer Lodge Basin of Southwestern Montana. In comparison, the costae of *P. tephrodes* differ in being quite constant in size, more closely spaced (12–14 per mm on last half of ultimate whorl), and consistently

much weaker and less prominent than the major riblets of *P. costatus*. The aperture of *P. costatus* ascends more strongly than that of *P. tephrodes* in the ultimate quarter whorl, and its peristome is more strongly everted and thickened within. *Pupoides montana* is larger, has a greater H/W ratio (ave. 2.29), and lacks riblets except on the last quarter whorl, where they occur directly behind a sharply terminated, unreflected peristome. *Pupoides costatus* differs from modern *Pupoides hordaceus* (Gabb, 1866) and *P. inornatus* Vanatta, 1915, in having shorter whorls, and in having widely spaced, very strong riblets separated by multiple fine costellae on later whorls.

Etymology.—*costatus*, Latin—ribbed.

Material.—More than 20 specimens. Holotype: CM-41634, and paratypes PPUP-139 (2 fragments) are from Wurtz Bend (NFF-19) locality, Flathead County, Montana, Kishenehn Formation, late Eocene-Oligocene. Additional paratypes: CM-41635 (3); KUMIP-289,714; KUMIP 290,715 (3); PPUP-134; PPUP-135 (plastitype); PPUP-136 (3, 1 plastitype) are from Commerce Creek (CMC-1) locality; PPUP-137 (3 fragments) is from E-5 (NFF-1) locality; PPUP-138 is from E-4 (NFF-2) locality (1 fragment); and PPUP-174 from W-2 (NFF-5) locality, all British Columbia. All localities in Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Pupoides tephrodes Roth, 1986
(Fig. 10.D, 10.E)

Description.—“Shell dextral, narrowly umbilicate, cylindrical with convexly low-conic summit, about 5.2 tall whorls; suture moderately impressed, crenulated by axial riblets. Early whorls convex; fourth and fifth whorls roundly shouldered below suture, compressed at periphery and anteriorly. Nuclear whorls 1.5, smooth; neanic sculpture of slender, well-spaced, retractive riblets. Body whorl narrowly, slopingly shouldered, compressed at periphery, slightly attenuated toward base, rising gently on penult behind aperture. Aperture oblique, ovate, peristome narrowly everted, not thickened within; parietal margin oblique, covered by a thin callus. No angular tubercle present.” (Roth, 1986:247). Costae (riblets) evenly spaced on earlier whorls, becoming quite crowded, about 12–14 per mm, on last half of ultimate whorl. Measurements of three hypotypes from locality E-2 (NFF-6) (with average and range of dimensions): height, ave. 3.2 mm (3.0–3.4); diameter, ave. 1.42 mm (1.40–1.45); H/D, ave. 2.26 (2.14–2.43); whorls, ave. 5.2 (5.1–5.25).

Discussion.—These specimens compare very well with the two paratypes of *Pupoides tephrodes* Roth, 1986 (USNM 377381) filed at the U. S. National Museum. Examination of these paratypes showed that the costae are regularly spaced on the penultimate and earlier whorls as is observed on the specimens from the Kishenehn Basin, that they also shared the observed characteristic of crowding of costae on the last half of the ultimate whorl, and, although broken back and lacking complete apertures, one appeared to have a shallow constriction of the ultimate whorl immediately behind the aperture.

Examination of a considerable number of Pleistocene and Recent *P. hordaceus* in the author’s reference collection showed that this crowding of the costellae is not a characteristic of *P. hordaceus*, and that the costae (riblets) of *P. hordaceus* are considerably stronger and somewhat more widely spaced than observed on the *P. tephrodes* specimens from either the Kishenehn or Three Forks basins.

Material.—Eighteen specimens. Figured specimen CM-41632, and hypotypes CM-41633 (3); KUMIP 289,712; KUMIP 289,713 (3); and PPUP-131 (7) are from E-2 (NFF-5) locality, British Columbia. Additional hypotypes are: PPUP-132 from Island (NFF-4) locality, British Columbia and PPUP-133 (2) from Moose City South (NFF-10) locality, Flathead County, Montana. All localities in Lower Member, Kishenehn Formation, late Eocene-Oligocene.

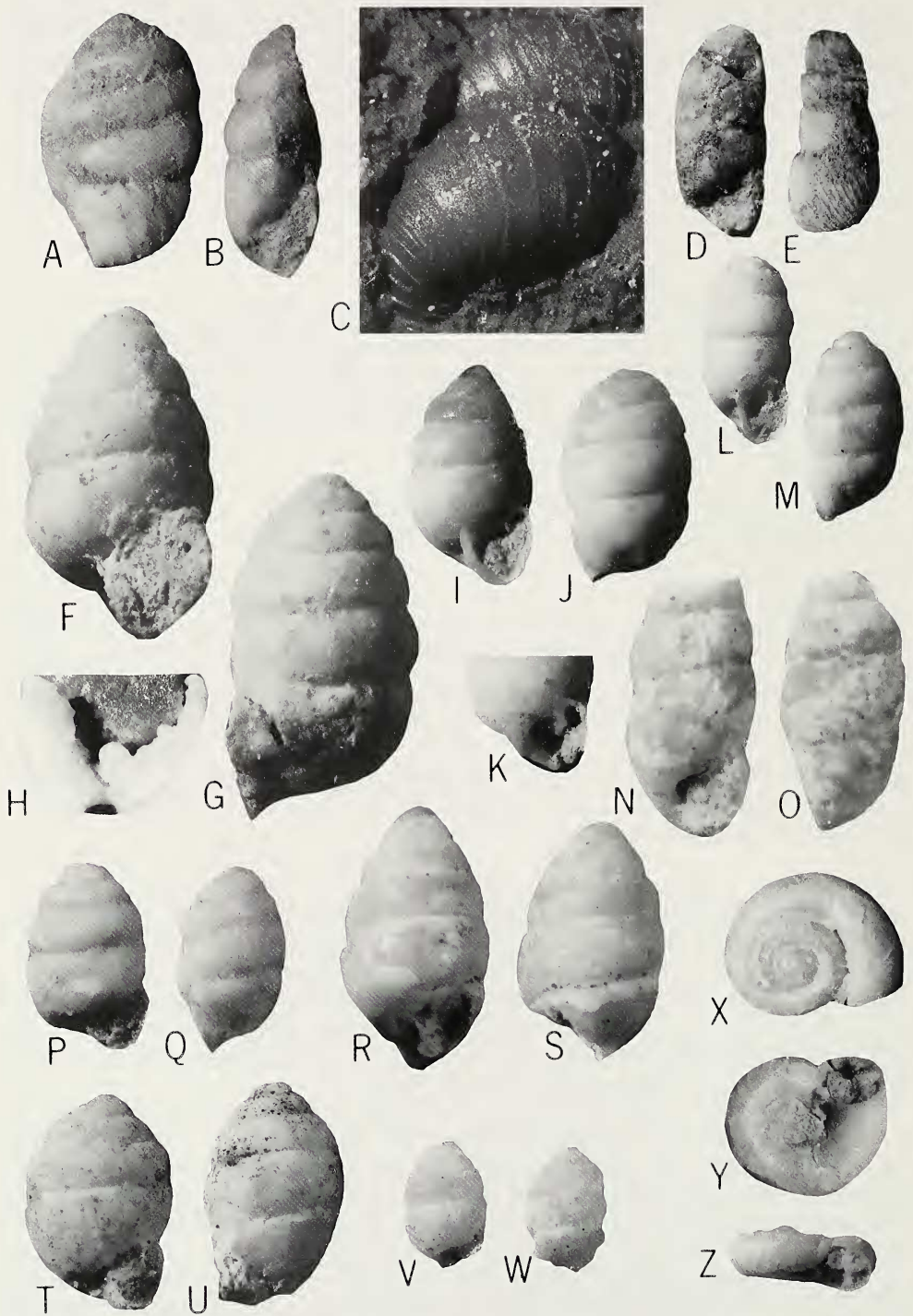


Fig. 10.—STYLOMMATOPHORA: PUPILLIDAE. A–C: *Pupoides costatus* n. sp. A–B: Holotype (CM 41634), X12, laterally compressed; A, apertural; B, lateral; C, *P. costatus* Plastitype (PPUP-135).

Subfamily Gastrocoptinae Pilsbry, 1948

Genus *Gastrocopta* Wollaston, 1878

Type species.—Pupa acarus Benson, 1856, by subsequent designation (Pilsbry 1916–1918).

Subgenus *Gastrocopta* s. str.*Gastrocopta minuscula* Pierce, 1992

(in Pierce and Rasmussen, 1992:46–47)

(Fig. 10.L, 10.M)

Description.—“Shell minute, rimate, cylindric, apex obtusely conic, whorls less than five, moderately convex, sutures well impressed, sculpture of fine growth striae; body whorl rounded to faintly keeled, aperture suboval, slightly ascending, peristome thin, narrowly reflected, without ridge or crest behind aperture; . . .” (Pierce and Rasmussen, 1992:46–47).

Emendation to description.—Minor crest behind aperture, flattened externally over palatal folds, teeth five (2:1:2); angulo-parietal lamella bilobed, chevron shaped, lobe at mid-length deflected abaxially, columellar lamella semi-discoidal, curved and descending to near vertical distally, palatal folds two, upper nodular, lower a deeply entering, elongate, erect, bluntly terminated semi-discoid. Range of measurements for hypotypes (N=14): height 1.5–1.9 mm; width 0.9–1.0 mm; H/W 1.58–2.00; whorls 4.5–4.8.

Discussion.—Among modern species, *G. minuscula* closely resembles Caribbean *G. pellucida* (Pfeiffer, 1841), differing in having only a small external dimple at the location of the lower palatal fold, essentially no crest, no basal fold, and a curved, descending columellar lamella. For further comparison, see Pierce and Rasmussen, 1992:47.

Environment and Distribution.—This species was known only as a fossil from the Cabbage Patch fauna, late Oligocene-early Miocene, of southwest Montana. The overall climate and environment reconstructed from the Cabbage Patch fauna is of a mixed shrubland (savanna) and woodland, seasonally wet and dry, with MAT of about 10°C, January mean probably not less than 5°C and July mean of about 15°C to 20°C and MAP near 50 cm. (Pierce, 1993:988–991). The modern analog, *G. pellucida*, in its various subspecies, is widely distributed in subtropical and tropical environments. It is found throughout the Antilles, Florida, with scattered colonies along the Atlantic Seaboard to Cape May, New Jersey, around the Gulf of Mexico generally at least to the Yucatan Peninsula (collected by senior author), across northern Mexico and southwestern United States to southern California, thence south throughout Baja California (Pilsbry, 1948:914; Smith et al., 1990:105–106). Modern *G. pellucida hordeacella* (Pilsbry, 1890) has been found in middle Pleistocene (Yarmouthian Interglacial) in North Texas (Pierce, unpublished data).

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X20 abapertural, detail of costae on plastotype; D, E: *Pupoides tephrodes* Roth, 1986, X10, D. Hypotype (CM 41632) apertural; E. Hypotype (KUMIP 289,712) apertural; F–H: *Gastrocopta kintlaense* n. sp. F–G: Holotype (CM 41640), X10; F. apertural; G. lateral; H. *G. kintlaense* Paratype (PPUP-151-2), X25, apertural detail; I–K: *Gastrocopta akokala* n. sp. I–J: Holotype (CM 41642) X15; I. apertural; J. lateral; K. *G. akokala* Paratype (PPUP-155a), X10, excavated aperture; L–M: *Gastrocopta minuscula* Pierce, 1992, Hypotype (CM 41636), X15; L. apertural; M. lateral; N–O: *Gastrocopta leonardi* Pierce, 1992, Hypotype (CM 41638), X15; N. apertural; O. lateral, incomplete specimen; P–Q: *Vertigo consteni* n. sp. Holotype (CM 41644), X15; P. apertural; Q. lateral; R–S: *Vertigo* sp, c.f. *V. arenula* White, 1876, Hypotype (CM 41646), X15; R. apertural; S. lateral; T–U: *Vertigo doliara* n. sp. Holotype (CM 41648), X15; T. apertural; U. lateral; V–W: *Vertigo micra* n. sp. holotype (CM 41649), X15; V. apertural; W. lateral; VALLONIDAE. X–Z: *Vallonia kootenayorum* n. sp. Holotype (CM 41651), X12; X. apical; Y. umbilical; Z. apertural X10.

Material.—More than 50 specimens. Figured specimen, CM-41636, and additional hypotypes: CM-41637 (3); KUMIP 289,716; KUMIP 289,717 (4); and PPUP-140 (7) are from Wurtz Bend (NFF-19) locality, Flathead County, Montana. Additional hypotypes are as follows: PPUP-141 (17 steinkerns) from Kintla Creek Carnegie (KTL-1) locality; PPUP-142 from Lower Kintla Rapids (NFF-18) locality; PPUP-143 from Kintla Creek River (NFF-17) locality; and PPUP-147 (2) from Moose City South (NFF-10) locality, all Flathead County, Montana; and PPUP-144 from Commerce Creek (CMC-1) locality (1 mold and plastitype); PPUP-145 from E-5 (NFF-1) locality; and PPUP-146 (7) from E-2 (NFF-2) locality, all British Columbia. All localities in Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Subgenus *Albinula* Sterki, 1892

Type species.—*Pupa contracta* Say, 1822.

Environment and Distribution.—Modern taxa of this subgenus are widely tolerant in both temperature and moisture requirements although there appears to be a slight bias to grassland environments. It is widely distributed in North America east of the Continental Divide and has been reported from eastern Canada to north central Mexico. Known geologic range is from late Eocene-early Oligocene (Chadronian) (Roth, 1986:241), then from late Pliocene (Blancan) to Recent. A similar subgenus, *Ameralbinula* Pierce, 1992 was found in a late Oligocene-early Miocene (Arikareean) fauna (Pierce and Rasmussen, 1992:42).

Gastrocopta kintlana Pierce, new species

(Fig. 10.F–10.H)

Diagnosis.—A small ovate-conic *Albinula* distinguished by a fused, sinuous L-shaped, angulo-parietal lamella, a sub-vertically oriented discoidal columellar lamella, and disparate palatal folds, upper small, tuberculate, lower massive, chisel-shaped in apertural aspect.

Description.—Shell dextral, narrowly umbilicate, ovate-conic, of about 5.5 well rounded whorls, suture well impressed. Nuclear whorls about 1.6, finely punctate, juvenile whorls initially sculpted with faint striae that become stronger and closely and evenly spaced by the third whorl, continuing to the reflected peristome. Last quarter whorl ascending slightly, moderately but roundly keeled, in basal aspect nearly straight, slightly constricted behind peristome, weak crest. Aperture advanced about 20° past axis, roundly triangular, projecting, thickened by interior callus, upper insertion near horizontal, connected to lower insertion by diagonal callus, peristome reflected moderately at straight to slightly sinuous outer lip, inner lip reflected more strongly. Teeth five or, occasionally, six, angulo-parietal lamella fused, sinuous, L-shaped, extending to plane of aperture, proximal end nearly connecting to peristome, projecting lobe near mid-length deflected adaxially, distal end curved abaxially, columellar lamella prominent, discoidal to roundly triangular, curves from sub-vertical to vertical distally, palatal folds two or three on callus, upper palatal small, nodular, shortly entering, lower palatal distinctively strong, chisel-like in apertural view, but tapering distally, more deeply entering than upper palatal, interpalatal not always present, thin, low, elongate ridge, descending diagonally to nearly join lower palatal. Dimensions of holotype: height 3.25 mm; diameter 1.8 mm; H/D 1.81; whorls 5.75; of paratype: height 2.8 mm; diameter 1.7 mm; H/D 1.65; whorls 5.25.

Discussion.—This species blends many of the variations in apertural teeth noted in the subgenus *Albinula*, and is especially similar to modern *Gastrocopta contracta* v. *climeana* Vanatta, 1911, differing in being larger, in having less massive dentition, especially the angulo-parietal lamella, and a weaker callus connecting the insertions of the peristome. Among fossil *Gastrocopta*, *G. kintlana* closely resembles Pliocene *G. proarmifera* Leonard, 1946, differing in being considerably smaller, having weaker dentition, and an L-shaped angulo-parietal lamella. It also resembles, in outline, more elongate specimens of Oligocene *G. obesa* Pierce, 1992, but the dentition of the latter, subgenus *Ameralbinula* Pierce, 1992, is very different. *Gastrocopta (Albinula) species a*, Roth, 1986, is also quite similar, dif-

fering in size, in shape of sinuous angulo-parietal lamella, in having a horizontal columellar fold, and, apparently, lacking a palatal callus. *Gastrocopta montana* Roth, 1986 is much smaller, has a strong crest behind the aperture, and a more sinuous angulo-parietal lamella. *Gastrocopta kintlana*, and Roth's *G. montana* and *G. (Albinula)* species *a*, are quite similar and, as Roth (1986:244) proposed, "*G. contracta* may be the surviving member of a once more diversified lineage."

Etymology.—Named for Kintla Creek, a tributary entering the Flathead River from Glacier National Park and flowing past the type locality.

Material.—About 30 specimens. Holotype, CM-41640, and paratypes: CM-41641 (3); KUMIP 289,718; KUMIP 289,719 (3); and PPUP-148 (15, crushed and fragments) are from Kintla Creek-River (NFF-17) locality, Flathead County, Montana, Kishenehn Formation, middle Eocene-late Oligocene. Additional paratypes: PPUP-149 from North Ford Creek (NFF-21) locality; and PPUP-150 from Wurtz (NFF-19) Bend locality, both Flathead County, Montana; and PPUP-151 (fragments) from E-5 (NFF-1) locality and PPUP-152 (2 fragments) from Commerce Creek (CMC-1) locality, both British Columbia. All localities in Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Gastrocopta akokala Pierce, new species

(Fig. 10.I–10.K)

Diagnosis.—A small ovate *Albinula* distinguished by a moderate to strong crest and a diagonal sulcus behind the aperture, a slightly bilobed, fused angulo-parietal lamella, and deeply entering lower palatal fold.

Description.—Shell small, rimate, ovate with obtusely conic apex, of about 4.75 to 5.25 rounded, nearly smooth whorls, suture moderately impressed, last whorl about same diameter as penultimate. Nuclear whorls about 1.6, smooth to very finely punctate, subsequent whorls have occasional, very weak striae that become more regular and noticeable on the last whorl, base of last half whorl distinctly pinched or keeled, flaring to roundly triangular aperture with reflected peristome, moderate to strong crest behind aperture and distinct exterior diagonal sulcus behind crest marking position of palatal folds. Aperture with five or more teeth, angulo-parietal lamella arising near insertion of outer lip and only scarcely behind plane of the aperture, slightly bilobed anteriorly, sinuous, medial lobe deflected abaxially, inner continuation spiral or diverging slightly from columella, columellar lamella a small, elongate, blunt disk, near horizontal, palatal folds on slightly thickened diagonal ridge reflecting exterior sulcus, upper short, nodular, lower deeply entering, erect oval blade, ascending slightly distally, a tiny suprapalatal or infrapalatal node may occur. Dimensions of holotype: height 2.1 mm; width 1.3 mm; H/W 1.62; whorls 4.8. Range of measurements: height 1.9–2.4 mm; width 1.1–1.45 mm; H/W 1.50–1.89; whorls 4.6–5.25.

Discussion.—*Gastrocopta akokala* is intermediate in size and shape between modern *G. holzingeri* (Sterki, 1889—*vide* Pilsbry, 1948:883) and *G. contacta* (Say, 1822), and its apertural characteristics more closely resemble *G. holzingeri*, differing in not having a strongly bifurcate angulo-parietal lamella. Among fossil specimens, *Gastrocopta akokala* appears most similar to the three albinulid species described by Roth (1986:241–244) from the late Eocene Bozeman Group of the Three Forks Basin of southwestern Montana. It differs from *G. montana* in being more ovate, lacking noticeable striae, having a stronger crest and deeper sulcus behind the aperture, and in shape and placement of the palatal folds; from *G. sagittaria* in being larger, ovate versus conical, having a smaller aperture, proportionally, and a strong crest and exterior sulcus; and from *G. (Albinula)* species *a* in being smaller, more ovate, with a strong crest behind the aperture, and an elongate lower palatal fold. *Gastrocopta akokala* superficially resembles, in shape, the considerably larger *G. obesa* Pierce, 1992, from the Oligo-Miocene Cabbage Patch Beds of the Renova Formation in the Deer Lodge and Flint Creek Basins of western Montana, but lacks the characteristic angulo-parietal lamella of the subgenus *Ameralbinula* Pierce, 1992.

Etymology.—Named for Akokala Creek, a tributary entering the Flathead River from Glacier National Park just downstream of the Wurtz Bend type locality of this species.

Material.—More than 100 specimens. Holotype, CM-41642, and paratypes: CM-41643 (10); KUMIP 289,720; KUMIP 289,721 (10); PPUP-153, PPUP-154 (10), and PPUP-155 (16) are from type locality, Wurtz Bend (NFF-19) locality, Flathead County, Montana, Kishenehn Formation, middle Eocene-late Oligocene. Additional paratypes: PPUP-156 (2 crushed) from South Ford Creek (NFF-22) locality; PPUP-157 (2 crushed) from North Ford Creek (NFF-21) locality; PPUP-158 (2 crushed) from Starvation Bend (NFF-12) locality; PPUP-159 from Bowman Creek (BWN-2) locality; PPUP-160 (3 fragments) Kintla Creek Carnegie (KTL-1) locality; PPUP-161 (8) from Lower Kintla Rapids (NFF-18) locality; and PPUP-162 (2) from Moose City South (NFF-10) locality, all Flathead County, Montana; and PPUP-163 (4 plastitypes), PPUP-164 (4), PPUP-165 (4 plastitypes), and PPUP-166 (mold and plastitype) from Commerce Creek (CMC-1) locality; PPUP-167 (5) from E-5 (NFF-1) locality; PPUP-168 (>20) from E-4 (NFF-2) locality; PPUP-169 (2) from E-3 (NFF-3) locality (2); and PPUP-170 (6) from E-2 (NFF-6) locality, all British Columbia. All localities in Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Subgenus *Vertigopsis*, Cockerell mss., Sterki, 1892

Type species.—*Pupa pentodon* (Say, 1821).

Gastrocopta sp., cf. *G. leonardi* Pierce, 1992,

(in Pierce and Rasmussen, 1992:46)

(Fig. 10.N, 10.O)

Discussion.—*Gastrocopta leonardi* resembles modern *G. pentodon* but is larger and lacks a basal fold and crest. Among fossil species, it most resembles "*Vertigo*" *praeoquis* Russell, 1956b, from the Miocene of Wyoming, but differs in being a third larger, and in having a broader, more rounded aperture that ascends distinctly in the last 60° of the ultimate whorl. These specimens can be easily separated from the remaining pupillid taxa, but their fragmentary nature precludes precise identification. There are, however, enough similarities to *G. leonardi* specimens, from its type locality, to warrant this identification.

Environment and Distribution.—This species is previously known only from the late Oligocene-early Miocene (Arikarean) Cabbage Patch fauna of southwest Montana. The overall climate and environment have been described under *Gastrocopta minuscula*. The subgenus is distributed from southeastern Canada and eastern United States south to Florida, west to a center of diversity in Arizona and south along the Gulf and Caribbean coast of Mexico to Guatemala (Pilsbry, 1948:886–891). Geologic range of the subgenus includes the late Oligocene-early Miocene (Arikarean) and are common in middle to late Pliocene (Blancan) faunas.

Referred material.—Four specimens. Figured hypotype is from CM-41638 (3), from Kintla Creek Carnegie (KTL-1) locality, Flathead County, Montana. Additional specimen CM-41639, from E-4 (NFF-2) locality, and one specimen, now lost, was from Commerce Creek (CMC-1) locality, both British Columbia. All localities in Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Subfamily Vertiginae Pilsbry, 1948

Genus *Vertigo* Müller, 1774

Type species.—*Vertigo pusilla* Müller, 1774.

Subgenus *Vertigo s. str.*

Environment and Distribution.—The subgenus *Vertigo s. str.* is widely distributed from eastern and northern Canada to California and northern Mexico. It is a very tolerant group, being found from Sea Level to 3,000 meters (10,000 feet), from cool moist to hot semiarid climates. The geologic range of the subgenus is Eocene to Recent, with *V. arenula* known from the Eocene and Oligocene. The

subgenus is common in middle to late Pliocene (Blancan) sediments of the mid-continent and west.

Vertigo consteniusi Pierce, **new species**

(Fig. 10.P, 10.Q)

Diagnosis.—A small, broadly ovate *Vertigo* with weak sculpture, roundly oval aperture with weak indentation on palatal margin, very long lower palatal fold.

Description.—Shell small, rimate, broadly ovate, of about 4.6 to 5.2 well-rounded whorls, suture moderately impressed, juvenile whorls about 1.4, smooth to finely punctate, subsequent whorls with weak, fine striae; last half whorl roundly keeled, ascending slowly in last 30°, shallow, elongate sinus behind aperture marks location of palatal folds; aperture roundly oval, peristome thin and sharp, reflected over basal margin, very weak marginal sinus on palatal margin, weakly developed crest extending from sinus to keel, outer lip above sinus near parallel to axis, below sinus retracted about 15°; teeth four or more, parietal lamella thin, erect blade, arising near middle of parietal margin, slightly behind plane of aperture, columellar lamella near horizontal, blunt discoid, palatal folds two or more, upper elongate node, lower more deeply entering, long, straight, proximal third an erect, rounded lobe, distal two-thirds lower, thinner, near horizontal. Dimensions of holotype: height 1.80 mm; width 1.20 mm; H/W 1.50; whorls 4.6. Range of measurements, including holotype (N=9): height 1.7–2.1 mm; width 1.1–1.2 mm; H/W 1.50–1.75; whorls 4.6–5.2.

Discussion.—*Vertigo consteniusi* appears to belong to the *V. gouldi* group (*sensu* Pilsbry, 1948:971). The presence or absence of an angular lamella or basal fold could not be established. It differs from typical *V. gouldi* (A. Binney, 1843) primarily in strength of striae and length of lower palatal fold. Among fossil species, it resembles closely both late Oligocene *V. whitei*, Pierce, 1992, from which it differs in size, sculpture, and in lacking(?) an angular lamella; and Eocene to late Oligocene *V. arenula* (White, 1876), from which it differs in size, very blunt apex, and an even longer lower palatal fold and lack(?) of angular lamella. Both of the latter also appear to belong to the *V. gouldi* group, despite the presence of angular lamellae.

Etymology.—*consteniusi*, so named to honor Norman and Lee Constenius, of Whitefish, Montana, dedicated paleontologists who supported in so many ways the field work for this study.

Material.—Thirteen specimens. Holotype, CM-41644, and paratype KUMIP 289,722, are from Wurtz Bend (NFF-19) locality. Additional paratypes: PPUP-171 is from Bowman Creek (BWN-2) locality; CM-41645 (3), KUMIP 289,723 (3), and PPUP-172 (5) are from Kintla Creek Carnegie (KTL-1) locality, all localities Flathead County, Montana and in Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Vertigo sp., cf. *V. arenula* (White, 1876)

(Fig. 10.R, 10.S)

Discussion.—Unfortunately, the apertures of all specimens are damaged or solidly blocked, precluding precise identification; however the shape of the shell, the H/W ratio, the sculpture, and the sinus behind the aperture strongly suggest *V. arenula*. These specimens are a little larger than White's (1876:46) description, 2 mm × 1.2 mm, (H/W 1.67) or that reported in the emended description by Pierce (Pierce and Rasmussen, 1992:47) of 2.14 mm × 1.25 mm, H/W 1.70, but closely approximate the measurements given by Yen (1946:500) of 2.5 mm × 1.5 mm (H/W 1.67). The close concordance of the H/W ratios is notable. Measurements of hypotype from E-3 (NFF-3) locality: height 2.50 mm; width 1.50 mm; H/W 1.67; whorls 5.3. It is possible that these specimens and those of Yen (1946:500) represent a distinct species, but the material at hand is inadequate to make this determination.

Environment and Distribution.—Fossil from Eocene (White, 1876:105, 131) to late Oligocene (Pierce, 1993:fig. 2). This species is believed to be adapted to a climate with at least 10°C Mean Annual Temperature (MAT), January MAT probably not less than 5°C, Mean Annual Precipitation 50 cm or less, and a grassland/shrubland vegetation (Pierce, 1993:990).

Material.—Seven specimens. Figured specimen: CM-41646 from E-3 (NFF-3) locality, British Columbia. Additional hypotypes: CM-41647 (3); KUMIP 289,724 (3) from E-2 (NFF-6) locality, both localities in British Columbia, Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Subgenus Indeterminate
***Vertigo doliara* Pierce, new species**
(Fig. 10.T, 10.U)

Diagnosis.—A small, extremely corpulent, oval *Vertigo* with a small, roundly triangular aperture.

Description.—Shell small, obtusely oval with blunt apex and base, of about five rounded whorls, suture shallowly impressed, nuclear whorls about 1.5, smooth, subsequent whorls with very weak striae; body whorl markedly narrower than penultimate whorl, ascends slightly on penultimate in last 45°, roundly keeled with long, diagonal sulcus, extending across the keel, marking the position of the lower palatal fold; aperture small, roundly triangular, parietal lamella thin blade, arising near middle of parietal margin, deflected very slightly abaxially, neither angular, if it exists, nor columellar lamella, nor upper palatal fold observed, lower palatal fold long, deeply entering, sweeping abapically across base of whorl. Dimensions of holotype: height 2.05 mm; width 1.45 mm; H/W 1.41; whorls 5.0.

Discussion.—This species probably belongs to the subgenus *Vertigo s. str.*, but lacks adequate diagnostic features to so assign with complete confidence. In shape it resembles several corpulent species from the southeast United States, such as *V. rugulosa* Sterki, 1890, but none achieve the extreme corpulence, H/W 1.41, of this species, nor its distinct blunt oval shape. Among fossil pupillids, only among the *Gastrocopta*, e.g., *G. sagittaria*, Roth, 1986, H/W 1.38, and *G. oviforma* Pierce, 1992, H/W 1.48, is this degree of extreme corpulence achieved. *Gastrocopta sagittaria* has a much larger aperture, and *G. oviforma* is much larger.

Etymology.—*doliara*, Latin, tubby, fat.

Environment and Distribution.—Unknown.

Material.—One specimen. Holotype: CM-41648 from Moose City South (NFF-10) locality, Flathead County, Montana, Kishenehn Formation, middle Eocene-late Oligocene.

***Vertigo micra* Pierce, new species**
(Fig. 10.V, 10.W)

Diagnosis.—A tiny ovate *Vertigo* with blunt apex and fine, distinct striae.

Description.—Shell tiny, about 1.2 mm in height, rimate, ovate with bluntly conical apex, of about 4.7 well-rounded whorls, suture moderately impressed, sculpture of fine, distinct, retractive striae, last 60° of ultimate whorl rises on penultimate whorl, details of aperture and dentition unknown. Dimensions of holotype: height 1.25 mm; width 0.85 mm; H/W 1.47; whorls 4.7. Dimensions of plastotype: height 1.15; width 0.75, H/W 1.53.

Discussion.—*Vertigo micra* is truly a pygmy among pygmies. The only other *Vertigo* of equal minuteness is modern *V. hebardii* Vanatta, 1912, which is a member of the subgenus *Vertigo s. str.*, and of the *Vertigo gouldi* group. The type material at hand, three steinkerns, all incomplete in the apertural area, and a cast, aperture not shown, are insufficient to determine precisely the taxonomic position

of *Vertigo micra*, but it appears highly likely that it is a member of the same subgenus and group. Among fossil *Vertigo*, *V. micra* is immediately distinguishable on the basis of size alone; no other fossil *Vertigo* is so minute. However, in shape, it bears a strong resemblance to both *Vertigo whitei* Pierce, 1992, from the late Oligocene Deer Lodge Basin of far western Montana, and to *Vertigo consteniusi*, which is found in association with *V. micra*, but it is immediately distinguishable from both on size alone. *Gastrocopta sagittaria* Roth, 1986, from the late Eocene Three Forks Basin of western Montana, bears considerable resemblance in shape of shell, but is, again, much larger.

Etymology.—*micra*, derived from *mikros*, Greek, small.

Environment and Distribution.—Unknown.

Material.—Four specimens. Holotype, CM-41649, a near complete steinkern and paratype, CM-41650 (2), are partial steinkerns from Kintla Creek Carnegie (KTL-1) locality, Flathead County, Montana. Paratype PPUP-173, a mold, with multiple plastotypes, is from Commerce Creek (CMC-1) locality, British Columbia. Both localities are in Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Family Valloniidae Pilsbry, 1900

Genus *Vallonia* Risso, 1826

Type species.—*Helix pulchella* Müller, 1774.

Vallonia kootenayorum Pierce, **new species**

(Fig. 10.X–10.Z)

Diagnosis.—Shell of the *Vallonia cyclophorella* Sterki, 1893 Group (*sensu* Pilsbry, 1948:1033), small, depressed, costate, aperture slightly descending, peristome weakly everted and thin, openly and eccentrically umbilicate.

Description.—Shell thin, depressed, of about 3.125–3.375 whorls, nuclear whorls about 1.5, finely granulose, neanic whorls 0.5, very faintly, finely, and irregularly costate, adult whorls ornamented with thin, thread-like, costae, with yet finer costellae between each pair, major costae continue onto base only slightly diminished, about ten costellae in last millimeter behind aperture; aperture descending slightly in last 15°, oblique, circular, peristome everted slightly, slightly thickened within; umbilicus wide, one-third major diameter, widening slightly in last one-half whorl. Measurements of holotype are: diameter, major, 2.05 mm; minimum, 1.75 mm; height 1.0 mm; H/W 0.49.

Discussion.—*Vallonia kootenayorum* is clearly a member of the *Vallonia cyclophorella* Group, ribbed, with a thin lip, and is most similar in size and sculpture to modern *Vallonia perspectiva* Sterki, 1893, from which it differs in having finer, more closely spaced costellae, an aperture that descends less, and it is consistently a little larger than average *V. perspectiva*. Taylor's (1960:77) report of the four oldest occurrences of *V. perspectiva* ranged through much of the Blancan NAL-MA (from mid-Pliocene? to early Pleistocene, ca. 5.0–1.5 Ma). *Vallonia kootenayorum* is from late Eocene-Oligocene strata occurring in the northern Kishenehn Basin. The only other mid-Tertiary North American *Vallonia* is *Vallonia berryi* Pierce, 1992, from the late Oligocene-early Miocene Cabbage Patch beds of southwestern Montana, 28–21 Ma. *Vallonia berryi* is a member of the very different *V. pulchella* (Müller, 1774) Group (Pilsbry, 1948:1023). The genus is known from Paleocene to Recent in Europe and Asia (Gerber, 1996:fig. 12). It is interesting to note that two of the three major North American valloniid groups (*V. pulchella* Group and *V. cyclophorella* Group) are represented in essentially modern form by the mid-Tertiary.

Etymology.—Named to honor the aboriginal Kootenay Indians that lived in this area.

Environment and Distribution.—The *Vallonia cyclophorella* Group originated in and is more generally distributed in the Mountain and Southwestern States and northern Mexico, but have spread spottily eastward throughout the Eastern United States (Pilsbry, 1948:1033–1037). Bequaert and Miller (1973:96–97; 191–192) describe *V. perspectiva* as a southwestern taxon, whereas *V. cyclophorella* is more montane in distribution. *Vallonia perspectiva* is characteristic of the Upper Sonoran and Transition Life Zones, whereas *V. cyclophorella* is more boreal, found in the Transition, Canadian and Hudsonian Life Zones. “*Vallonia perspectiva* is a closely related sibling of *V. cyclophorella*, . . . both being clearly derived from a common ancestor” (Bequaert and Miller, 1973:96). Previously known geologic range of the *V. cyclophorella* Group is rather brief, from late Pliocene (Blancan) to Recent (Taylor, 1960:77).

Material.—Thirty specimens. Holotype CM-41651 and paratype PVAL-110 are from Wurtz Bend (NFF-19) locality, Flathead County, Montana. Additional paratypes: PVAL-107 (7) from Commerce Creek (CMC-1) locality; PVAL-112, KUMIP 289,725 and KUMIP 289,726 (5) from E-4 (NFF-2) locality, both British Columbia; CM-41652 (9) and PVAL-108 from Kintla Creek Carnegie (KTL-1) locality; PVAL-109 (20 crushed) from Kintla Creek River (NFF-17) locality; and PVAL-111 from Bowman Creek (BWN-2) locality, all Flathead County, Montana, and all Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Superfamily Rhytidoidea Pilsbry, 1895

Family Haplotrematidae Baker, 1925

Genus *Haplotrema* Ancey, 1881

Type species.—*Helix durantii* Newcomb, 1864.

Haplotrema simplex (Russell, 1956), **new combination**

(Fig. 9.G–9.H)

Anguispira simplex Russell, 1956:111, fig. 5, plate 2, plate 3, fig. 1–3.

Diagnosis.—A small *Haplotrema* with weak radial wrinkles and without spiral striae.

Description.—Shell depressed, of about 5.5 broadly rounded, regularly expanding whorls, suture well impressed, umbilicus broadly open; surface glossy to waxy, light brown, embryonic whorls about 1.75, smooth, subsequent whorls with weak, low, irregular, discontinuous radial wrinkles, lacking spiral striae, aperture wider than tall, lip narrowly expanded, very slightly thickened. Measurements of hypotype (somewhat distorted): width 13 mm; height estimated 6 mm; H/W (est.) 0.46; whorls 5.5.

Discussion.—Considering the fact that this genus is almost unknown as a fossil, its presence in this Oligocene age Kishenehn Fauna is exciting. The oldest fossil occurrence of this genus personally known are Wisconsinian age fossils from a terrace deposit from western Virginia. F. C. Baker (1920a:389; 1920b:456) mentions occurrences in Sangamonian age sediments in the Mid-continent. It is a huge jump in time back to the Oligocene, and remarkable to find specimens that so clearly belong to the living genus. Russell's (1956:111, fig. 5, plate 2, fig. 1–3) holotype (GSC 11610) is a peculiarly compressed and distorted specimen that is difficult to recognize as an *Haplotrema*. However, his two paratypes (GSC 11611 and 11612, *loc. cit.*, Plate 2, figs. 4–6 and plate 3, fig. 1–3) are much more recognizable as *Haplotrema*, and either would have been more appropriate as holotype. The figured hypotype, also a topotype, is only slightly distorted and shows dorsal surfaces only, being imbedded in a matrix slab. It is too fragile to risk excavating the base of the specimen. The characteristic open umbilicus of this genus is obvious on other detached specimens.

In Roth's (1991) phylogenetic analysis of North American haplotrematids, 25

character states were analyzed, only four of which were of paleontologic value (Roth, 1991:163). His derived cladogram was used in substantiating a revision of the classification of the Haplotrematinae into two genera, *Ancotrema* H. B. Baker, 1930a, and *Haplotrema*, with three subgenera under the latter, and in deriving an approximate age of 42.5 Ma (late middle Eocene) for the divergence of the "temperate Haplotrematinae and its tropical out-group, the Austroselinitinae, . . ." (Roth, 1991:160). Based on the four shell characters used by Roth (1991:163), *Haplotrema simplex* fits neatly into the cladogram (Roth, 1991:fig. 3) as an (the?) ancestral species for the genus *Haplotrema*, with characteristics common to all three subgenera recognized, and sharing a sculpture pattern in common with *H. minimum* (Ancey, 1888), *H. vancouverense* (Lea, 1839—*vide* Pilsbry, 1946:221), *H. keepi* (Hemphill, 1890), and *H. concavum* (Say, 1821). It differs from each of the above in Character No. 25, not having "minute, close, wavy spiral striae" (Roth, 1991:163).

Environment and Distribution.—The genus is widespread in North America with distinct eastern and western Groups (Pilsbry, 1946:204–225; Roth, 1991). It appears to be equally tolerant in environment, from cool, moist of Alaska and British Columbia to warm dry of California and Baja California (Pilsbry, 1946, *loc. cit.*). A southern group, composed of the subgenus *Haplotrema s. str.*, and *H. caelatum* have a pattern of distribution that is dominantly in the Coast Ranges from the San Francisco area into Baja California (Pilsbry, 1946:204–225). As a genus, it is known as fossil only from the late Pleistocene eastern United States (LaRocque, 1970:606).

Material.—Fourteen specimens. Hypotypes (topotypes): CM-41653; KUMIP-289,727; and PHPL-101 all from E-4 (NFF-2) locality, British Columbia. Additional hypotypes, CM-41654 (2); KUMIP-289,728 (2); and PHPL-102 (2) all from E-5 (NFF-2) locality; and PHPL-103 from Commerce Creek (CMC-1) locality, all British Columbia, and PHPL-104 (4) from Starvation Bend (NFF-12) locality, Flathead County, Montana. Type horizon is Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Superfamily Bulimuloidea Tyron, 1867

Family Urocoptidae Pilsbry and Vanatta, 1898

Subfamily Eucalodiinae Crosse and Fischer, 1872

Genus *Holospira* von Martens, 1860

Type species.—*Cylindrella goldfussi* Menke, 1847, ICZN Opin., 1932.

Subgenus *Haplocion* Pilsbry, 1902

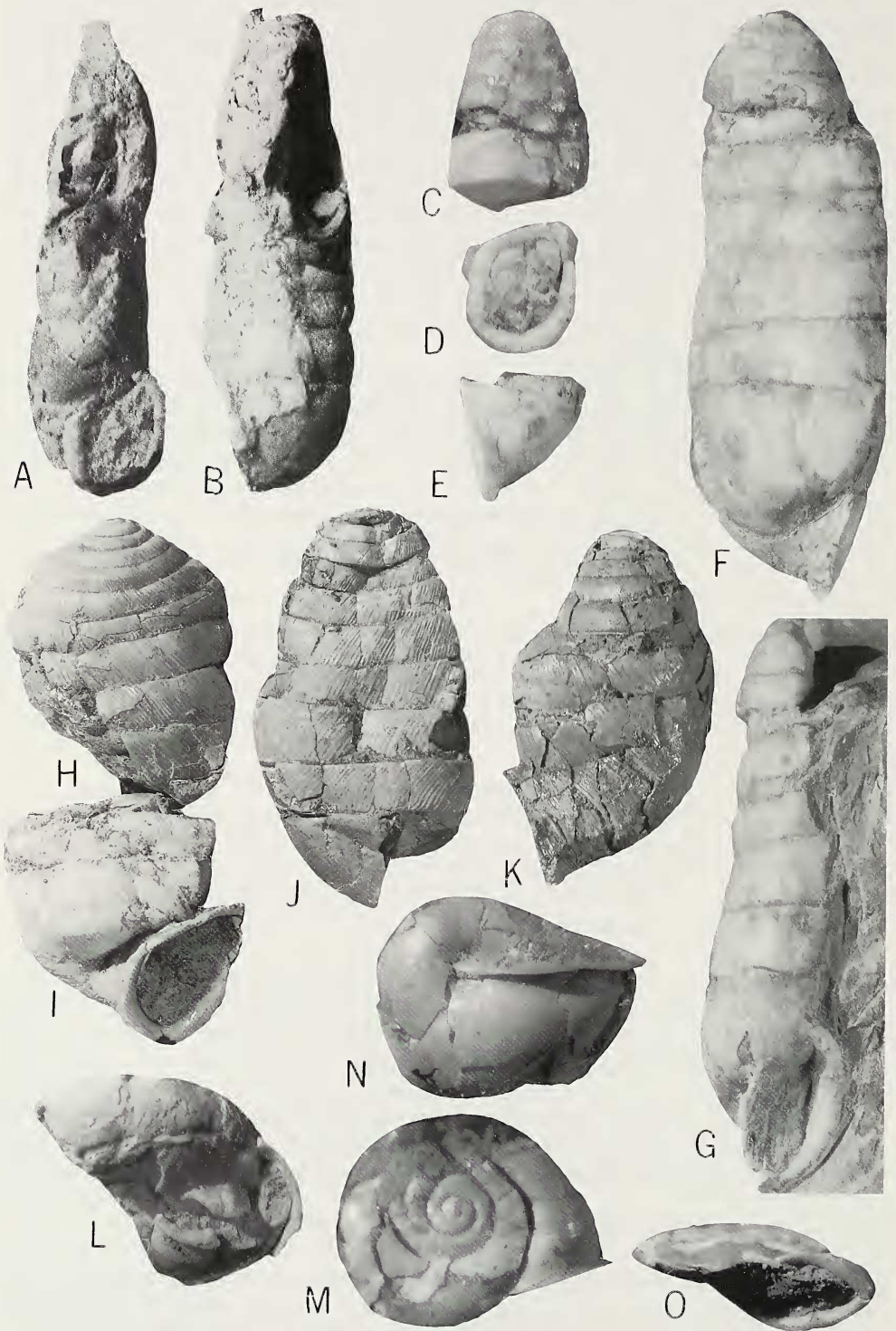
Type species.—*Holospira pasonis* Dall, 1895a.

Environment and Distribution.—The subgenus *Haplocion* is well adapted to existence in a warm, dry to arid environment. This group is distributed through southwest Texas and the northern Mexican states of Chihuahua, Coahuila, and Durango at moderate elevations to about 1,500 meters, with one species also reported from the Yucatan Peninsula (Bartsch, 1906:143; Pilsbry, 1953:151). Known geologic range of the subgenus is from Eocene (*H. plumbea* Roth and Megaw, 1989) to Recent, and, for the genus, from Cretaceous (*H. dyeri* Tozer, 1956) to Recent, with many species occurring during the Eocene and Oligocene.

Holospira tabrumi Pierce, **new species**

(Fig. 11.A–11.E)

Diagnosis.—A small *Haplocion* with prominent, well-spaced riblets on the body whorl, aperture a crudely pear-shaped oval with subparallel columellar and outer lips, peristome complete, strongly reflected, free of penultimate whorl.



Description.—Apical whorls six, conic with rounded summit, embryonic whorls two+, smooth, rapidly expanding, next four whorls expanding regularly, well sculptured with fine but strong and regular prosocline costulae, subsequent four or more whorls cylindrical, diameter about 4.5 mm, penultimate and antepenultimate whorls about 1.4 mm between sutures, bearing round-topped prosocline costae, body whorl 5.0 mm tall excluding reflected lip, bearing prominent, well-spaced, round-topped, slightly sinuous riblets spaced at about six riblets per millimeter on body whorl opposite aperture, umbilicus rimate to narrowly open, columella thin, minutely hollow; aperture projected and free of penultimate whorl, plane subparallel to axis, crudely oval pear-shaped with palatal and columellar margins subparallel, basal margin well rounded, merger of palatal and parietal margins roundly acute, peristome entire, widely reflected and strongly reinforced. Measurements: height (estimated) >15 mm; width of penultimate whorl, about 4.5 mm; height of aperture on palatal margin 4.2 mm, on columellar margin 3.4 mm; width 3.5 mm.

Discussion.—Although no one specimen is complete, all have the essential characteristics of the subgenus *Haplocion*. Among modern species, the aperture and last whorls of *H. tabrumi* most resemble *H. pasonis* Dall, 1895, but is much smaller. Among fossil taxa, it is similar in profile to *H. beardi* n. sp., but *H. beardi* has finer, more closely spaced, round-topped costae on the body whorl, 10–12 per mm, and an aperture appressed to the penultimate whorl, the plane of which is retractive from the axis by about 25°, and a weakly reinforced and reflected interrupted peristome. Eocene *H. plumbea* Roth and Megaw, 1989, is very similar, but differs from *H. tabrumi* in being larger with a more fusiform outline, has weaker sculpture on the body whorl, an aperture whose plane deviates from the axis by 20°–35°, and peristome continuous although appressed to the penultimate whorl. It differs from *Coelostemma dawsonae* n. sp., and all other fossil *Holospira*, in being much smaller, in having weaker costae on penultimate and antepenultimate whorls, which become strong and obvious on the body whorl, and in having a roundly pear-shaped projected aperture.

Etymology.—Named to honor Alan Tabrum, vertebrate paleontologist with the Carnegie Museum of Natural History, with whom I have worked in this project.

Material.—More than 13 specimens, most incomplete or fragmentary. Holotype CM-41655, and paratypes CM-41656 (2); KUMIP 289,729; KUMIP 289,730 (2); PURC-101-106 are from W-2 (NFF-5) locality, British Columbia, Lower Member, Kishenehn Formation, late Eocene-Oligocene. An apical fragment of seven whorls, PURC-107, from Moose City South (NFF-11) locality, Flathead County, Montana, same horizon, is provisionally referred to this species.

Subgenus *Haplocion*(?) Pilsbry, 1902
Holospira beardi Pierce, **new species**
 (Fig. 11.F, 11.G)

Diagnosis.—A small, conical-cylindric *Holospira*, aperture ovate, attached to penultimate whorl on parietal margin, peristome discontinuous, plane of aperture about 25° from axis.

Description.—Shell small, cylindric-ovate with 12 or more whorls, embryonic whorls about two,

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Fig. 11.—STYLOMMATOPHORA: UROCOPTIDAE. A–E: *Holospira tabrumi* n. sp. A, B: Holotype (CM 41655), X5; A. apertural; B. lateral; C–E: Paratype (CM 41656 lot), X4; C. apical fragment; D. apertural fragment, frontal; E. apertural fragment, lateral; F–G: *Holospira beardi* n. sp. Holotype (CM 41657), X5; F. lateral; G. apertural; H–K: *Coelostemma dawsonae* n. sp. X3; H–I: Paratypes, reconstruction composed of PURC-108, apical fragment, dextral, and KUMIP 289731, apertural fragment, dextral; J: Paratype KUMIP 289732, sinistral; K: Holotype CM 41658, dextral. POLYGYRIDAE. L. *Ashmunella? hilli* n. sp. Holotype (CM 41671), X5, apertural fragment with parietal lamella; M–O: *Praticolella lucifera* n. sp. Holotype (CM 41669), X5; M. apical; N. umbilical; O. apertural.

smooth, next four whorls with fine prosocline costellae becoming less pronounced on cylindrical whorls, then more pronounced on last two whorls with about 10–12 costae per millimeter on body whorl. Apical six whorls rapidly expanding, beehive-shaped, later whorls near cylindrical, exposed height of antepenultimate and penultimate whorls about 1.9 mm, body whorl about 5 mm in height, slightly constricted behind aperture, roundly keeled, umbilicus rimate. Aperture “U” shaped, peristome broadly reflected and strongly reinforced, but not continuous over penultimate whorl between insertions, parietal insertion much above columellar insertion, meeting penultimate whorl at about 60° near mid-point, bending rapidly to parallel axial plane, basal lip well rounded, plane of aperture retractive at about 25° from axis of shell, no lamellae detected; columella shallowly spiral and minutely hollow. Dimensions of holotype: height (including expanded lip), 15.25 mm; width (specimen slightly crushed) of penultimate whorl, estimated, 4.0 mm; exterior height of aperture at parietal insertion, 4.8 mm; at columellar insertion, 3.5 mm; width (slightly deformed), 2.9 mm.

Discussion.—The embryonic whorls of the essentially complete holotype are slightly damaged, but are definitely not mammillate. This species seems to blend the characteristics of several genera and subgenera from among the Urocoptidae. The slender, minutely hollow columella, along with the retained spire and smooth embryonic whorls argues for placement in the Holospirinae and the genus *Holospira*, whereas the incomplete peristome suggests relationship to the Microceraminae Pilsbry, 1904. Among modern species of *Holospira*, the most similar are of the subgenus *Haplocion* Pilsbry, 1902, as later redefined (Pilsbry, 1953:151), or *Allocoryphe* (Pilsbry, 1946). *Holospira pasonis* Dall, 1895, type species for *Haplocion*, differs from *H. beardi* in being larger, having a more convex profile, and a peristome complete and free of the penultimate whorl. *Holospira minina* von Martins, 1897, type species for *Allocoryphe*, is smaller, strongly ribbed and also has a peristome complete and free of the penultimate whorl.

Among fossil taxa, *H. beardi* apparently coexisted with and most resembles *H. tabrumi*, but *H. tabrumi* differs in bearing coarser costae, six per mm on body whorl opposite the aperture, and an aperture with complete peristome free of the penultimate whorl, the plane of which is subparallel to the axis. *Coelostemma dawsonae* n. sp., found at nearby localities, is larger, has fewer whorls, and a very different aperture. Cretaceous *H. dyeri* Tozer, 1956 is much larger and differs in nearly all aspects. Eocene *H. grangeri* Cockerell, 1914 appears about the same size, but has a more fusiform outline, and is too incomplete to merit further comparison. Oligocene *H. eva* Gardner, 1945, is similar, but larger, and has a continuous peristome that is adnate to the penultimate whorl. The enigmatic *Pupa? leidy* is also about the same size, but lacked the aperture and has now been lost. White's (1886:27, plate 5, figures 8–10) *Pupa? leidy* Meek, 1873, which may or may not be the same, is similarly convex, and has a projected peristome free of the penultimate whorl. La Rocque's (1960:49) Paleocene specimens of *Holospira* cf. *H. leidy* are too imperfect for other than tentative assignment to genus. Eocene *H. plumbea* Roth and Megaw, 1989, is very similar, but differs from *H. beardi* in being larger with fewer whorls, having a more fusiform outline, and a peristome continuous although appressed to the penultimate whorl. In apertural character, *H. plumbea* seems to occupy an intermediate position between the primitive(?) aperture of *H. beardi*, and the produced aperture with peristome complete and free of the penultimate whorl of *H. tabrumi* and typical of the modern subgenus *Haplocion*.

Etymology.—Named to honor Chris Beard, Curator of Vertebrate Paleontology at the Carnegie Museum of Natural History, with whom I have shared work and laughs on this project.

Material.—One specimen. Holotype: CM-41657, W-2 (NFF-5) locality, British Columbia, Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Genus *Coelostemma* Dall, 1896

Type species.—*Holospira elizabethae* Pilsbry, 1889.

Subgenus *Coelostemma* s. str.

Coelostemma dawsonae Pierce, **new species**

(Fig. 11.H–11.K)

Diagnosis.—A large, squat, ambidextrous *Coelostemma* with costulae/costae on all whorls after smooth, rounded embryonic whorls.

Description.—Shell large, squat, cylindrical to slightly fusiform with roundly conical apex, ambidextrous, both dextral and sinistral morphs found in association; embryonic whorls 2.0 to 2.2, rapidly expanding, smooth, somewhat protruding and rounded, subsequent four apical whorls expanding with fine, closely spaced, sweeping prosocline costulate, becoming more widely spaced, sharp-topped costae on cylindrical body whorls, with about five costae per mm on body whorl, body whorl about 5 mm tall, penultimate and antepenultimate whorls each about 2.5 mm between sutures; umbilicus narrowly open, columella large, hollow, almost $\frac{1}{2}$ diameter of shell; body whorl with rounded base, straightening and projecting forward, slightly constricted laterally behind roundly pear-shaped aperture, aperture about 7 mm tall and 6 mm wide, peristome complete, free of penultimate whorl, well reinforced and reflected on palatal and basal margins, less on parietal and columellar margins, no apertural lamella observed. Measurements of dextral holotype (crushed): height (estimated) >17.5 mm; width (at eighth whorl) 8 mm; whorls 10.5. Measurements of sinistral paratype (crushed): height (estimated) >19.0 mm; width (at eighth whorl) 7.5 mm; whorls >11.

Discussion.—Among living taxa, *C. dawsonae* most resembles the group of southwestern Mexican *Coelostemma*, differing in presenting a squatter profile as a result of fewer whorls and a slightly greater diameter of the cylindrical body. Among fossil taxa, the general size matches *Holospira adventica* Russell, 1956, which he found at two nearby Canadian localities (Russell, 1956:110), but both localities are now either destroyed or covered by slumping. *Holospira adventica* differs greatly from *C. dawsonae* in apertural character, in that its aperture is appressed to the penultimate whorl, peristome incomplete and/or interrupted by a prominent superior (parietal?) lamella, and it has an unusually tall body whorl, characters not characteristic of holospirids. *Holospira grangeri* Cockerell, 1914 is smaller and more slender. *Holospira eva* Gardner, 1945 is much taller and has a more elongate profile. Pilsbry (1953:139–140) determined that *H. eva* belongs in *Holospira* s. str. *Holospira dyeri* Tozer, 1956 is much taller, has a decidedly bullet-shaped profile, and differs in almost all characters. The enigmatic *Pupa? leidy* Meek, 1873, although never figured, is, by the original description, a shorter, narrower shell (14 mm \times 5 mm), with about 15 whorls (Meek, 1873:517).

Etymology.—Named to honor Mary Dawson, Curator of Vertebrate Paleontology at the Carnegie Museum of Natural History, with whom I have shared many an outcrop in seeing this project to a conclusion.

Environment and Distribution.—The genus *Coelostemma* is well adapted to existence in dry to arid environments. Its geographical distribution is unusual, one group is found in the high arid areas of the states of Coahuila and Nuevo Leon in northeastern Mexico, whereas a second group, isolated from the first by some 750 km, is found in similar terrain in the states of Guerrero and Oaxaca of southwestern Mexico. *Coelostemma dawsonae* most resembles the latter, and more distant, group. Geologic range of the genus is uncertain. Roth and Megaw (1989: 7) suggested that the enigmatic *Pupa? leidy* may be a *Coelostemma*. If so, the geologic range of the genus would have included the Eocene.

Material.—More than 20 specimens. Holotype, dextral: CM-41658; paratypes, dextral: KUMIP-289731; PURC-108; PURC-110 (7 apices); PURC-111 (3 fragments); and PURC-114(8); and para-

types, sinistral: CM-41659; KUMIP-289732, PURC-109, are from Starvation Bend (NFF-12) locality, Flathead County, Montana, Lower Member, Kishenehn Formation, late Eocene-Oligocene. Additional specimens, apical fragments of three or fewer whorls, and probably assignable to this taxon, are as follows: PURC-112, from E-3 (NFF-3) locality; and PURC-113 (4) from E-4 (NFF-2) locality, both in British Columbia, same horizon.

Superfamily Arionoidea Gray, 1840

Family Discidae Thiele, 1931

Genus *Discus* Fitzinger, 1883

Type species.—*Helix ruderata* H. and A. Adams, 1857.

Discus mackenziei Russell, 1956a

(Fig. 9.M)

Discussion.—Russell (1956a:111–112, figure 6, plate 3, figs. 4–6) found this species rather rare and only at his Locality E-4. His restoration in his Figure 6 appears generally accurate, although somewhat more depressed and flattened than justified by either his type material or the specimens collected on this project. Russell (*loc. cit.*) compared *D. mackenziei* to living *D. patulus* (Deshayes, 1830). Without a bit of care and caution, *D. mackenziei* can be easily confused with its fellow discid, *Anguispira*, cf. *A. alternata*, which is found at other localities in this area. The easiest way to separate incomplete or immature shells of the taxa is in the embryonic and neanic whorls. For *Anguispira*, cf. *A. alternata*, the nucleus is rather strongly produced above the subsequent whorl, the nuclear diameter is 0.5 mm, and the diameter of an immature or broken back specimen at 3.5 whorls will be 6.5 mm, or more. For *D. mackenziei*, the nucleus is scarcely elevated above the subsequent whorl, the nuclear diameter is less than 0.4 mm, and the diameter at 3.5 whorls is about 4.5 mm. This size difference is proportional throughout. At any given whorl, the whorl diameter for *D. mackenziei* will be noticeably smaller than at the same whorl locality for *Anguispira*, cf. *A. alternata*, and the costulae of *D. mackenziei* are finer and more closely spaced.

Environment and Distribution.—The modern genus is Holarctic, widely spread across the northern States and Canada, with relict populations extending south in the mountains of the East and Southwest and, in general, prefers cooler, moist climates and wooded environments (Hubricht, 1985:19, 20, 106–109; Pilsbry, 1948:598–622). Extant species are known from the mid-Pliocene of Wyoming and the late Pliocene of Nebraska (both Blancan). Fossil species are known to range from upper Cretaceous (as *Gonyodiscus* Fitzinger, 1833) through Miocene (Pilsbry, 1948:599) and Recent.

Material.—Two specimens and fragments. Figured specimen, KUMIP-289,733 (1+fragments), and additional hypotypes: CM=41660 (1); and PDIS-101 (fragments) are from E-4 (NFF-2) locality, British Columbia. Additional hypotype, PDIS-102 (fragments) from Kintla Creek-Carnegie (KTL-1) locality, Flathead County, Montana. Both locations are in the Lower Member of the Kishenehn Formation, late Eocene-Oligocene.

Genus *Anguispira* Morse, 1864

Type species.—*Helix alternata* (Say, 1816).

Anguispira sp., cf. *A. alternata* (Say, 1816)

(Fig. 9.N–9.P)

Description.—Shell depressed heliciform, sub-lenticular, openly umbilicate, about $\frac{1}{3}$ of diameter, with six or more rounded whorls; embryonic whorls about 1.5, first whorl smooth to faintly cross-hatched, with weak procline wrinkles on last half whorl, neanic whorls with distinct, regular, riblets,

somewhat carinate, becoming more rounded on later whorls; aperture unknown, shell material bleached, no evidence of flame-like blotches. Measurements of hypotype: height ± 8.5 mm; width >16 mm, estimated 18 mm; H/W (est.) 0.47; whorls >6 .

Discussion.—The largest specimens are usually quite abraded and the riblets are not well detailed. Smaller, juvenile or broken shells have embryonic whorls and riblet patterns that are not distinguishable from the modern species (Fig. 9. O,P; KUMIP 289,734). Despite the lack of a complete shell, or of a usable aperture, there appears essentially no doubt that, conchologically, these specimens are within the normal range of variability of Recent *A. alternata* (*s. lat.*), and is therein so placed, albeit reluctantly. F. C. Baker (1920:389) reports this species from strata as old as “Aftonian”, but the oldest occurrence of the species with which the author is personally aware is the University of Nebraska State Museum locality NO-104, Nuckolls, County, Nebraska, dated as late Kansan (ca. 600 Ka) on the basis of the immediately underlying Pearlette Type O ash. In either event, there is a huge time gap between these Kishenehn specimens and the Pleistocene occurrences. The distributional anomaly is just as great. Recent *A. alternata* is definitely an eastern taxon, not being found west of about 97° West longitude, but is distributed over a wide range of latitude and climate zones, from eastern Canada to coastal Texas (Pilsbry, 1948:569).

A. holroydensis Russell, 1956a from the Upper Miocene North Park Formation of southeastern Wyoming has fewer whorls, four, is smaller, diameter 7.9 mm, and has subangular periphery, all characteristics of an immature or broken back specimen. Russell commented that, “Shells very similar to the present ones in appearance are found in the living *Anguispira alternata* (Say) and *A. cumberlandiana* (Lea)” (Russell, 1956a:1262). Paleocene *Anguispira russelli* Tozer, 1956, from photographs and description (Tozer, 1956:84–85, plate 8, figs. 10a–10c), also appears to fall within the range of variation of the Recent species, and differs from these Oligocene specimens only in having somewhat fuller, more rounded whorls. Not having seen the type material for either of these species, I do not include them in synonymy, although I strongly suspect they so belong. In any event, a species of land snail that has apparently resisted morphological change for 60 Ma would certainly be remarkable.

Environment and Distribution.—The living species is widely distributed in eastern North America, generally east of the 100th meridian and north of the 35th parallel into southern Canada (Hubricht, 1985:104). “A prolific, ubiquitous, and hardy snail favoring woodlands, especially of deciduous trees, but able to live in drier, more open woods or fields” (LaRoque, 1970:671). The geologic range of the genus is not clear. Species appearing to be essentially identical conchologically are found in Paleocene (*A. russelli*) and Miocene (*A. holroydensis*). The species is previously known as fossil from middle Pleistocene to Recent.

Material.—Nine specimens. Figured specimens: CM-41661, a large, worn specimen, is from Commerce Creek (CMC-1) locality, British Columbia, and KUMIP-289734 is from Wurtz Bend (NFF-19) locality, Flathead County, Montana, both Kishenehn Formation. Additional specimens: CM-41662, and PDIS-104 are from Starvation Bend (NFF-12) locality; KUMIP-289735, and PDIS-103 (2 fragments) are from Wurtz Bend (NFF-19) locality; and PDIS 105 is from South Ford Creek (NFF-22) locality, all Flathead County, Montana, and all are Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Superfamily Limacoidea
 Family Limacidae Gray, 1824
 Genus *Deroceras* Rafinesque, 1820
Type species.—*Limax laevis* Müller, 1774.
Deroceras mahiz Pierce, 1992
 (Fig. 9.K, 9.L)

Discussion.—The specimens from the Kintla Creek-River locality are essentially indistinguishable from the type material from the lower Cabbage Patch Beds (ca. 28 Ma) of the Deer Lodge Basin of southwestern Montana. These specimens generally retain at least part of their chalky outer layer, suggesting little or no transport. Larger plates (<2.5–3 mm) from most of the other localities tend to have a somewhat more rounded and less projecting base than observed in the Cabbage Patch type material or in the specimens from the Kintla Creek-River locality, and their basal yellow crystalline calcitic layer is somewhat thinner. Such minor variation is not thought to have taxonomic significance. These specimens somewhat resemble *D. aenigma* Leonard, 1950, but *D. mahiz* can be easily distinguished by its greater size, in having the nucleus more centrally located at the posterior margin, and in lacking the notch that is found beneath its nucleus. Small (~1 mm), circular, yellow calcitic disks, with or without a chalky dorsal surface, becoming elongate (1mm × <2mm) with growth, found at several localities are believed to be embryonic plates of this species.

Environment and Distribution.—Genus is of Holarctic distribution plus South America (LaRocque, 1970:664). Pilsbry's (1949:539) *Deroceras laeve* (Müller, 1774) Group is a plausible modern analog and probable descendant. Species of this Group are distributed from Alaska and Baffin Island to Central America (Pilsbry, 1949:539–557), and prefer humid areas like floodplains and marshes but can survive in drier conditions with some protection from desiccation (LaRocque, 1970:667). This species was previously known only from the late Oligocene Cabbage Patch Fauna (late Arikareean) of southwestern Montana (Pierce, 1992). As a genus, it is well represented from Oligocene to Recent.

Material.—More than 40 specimens. Figured specimen: CM-41665, and additional specimens CM-41666 (5), and KUMIP-289738 (5), are from Kintla Creek-River (NFF-17) locality. Additional specimens: PLIM-114 (17) from Commerce Creek (CMC-1) locality; PLIM-115 (4) from E-4 (NFF-2) locality; PLIM-116 from W-2 (NFF-5) locality, all British Columbia; KUMIP-289737 and PLIM-117 (7) from Starvation Bend (NFF-12) locality; PLIM-118 from Wurtz Bend (NFF-19) locality; PLIM-119 (4) from Lower Kintla Rapids (NFF-18) locality; PLIM-120 from Bowman Creek (BWN-2) locality, all Flathead County, Montana. All localities in Lower Member, Kishenehn Formation, late Eocene-Oligocene. Most of the PLIM specimens are very small, embryonic to immature.

Deroceras securis Pierce, 1992
 (Fig. 9.I, 9.J)

Discussion.—As was the case with *Deroceras mahiz*, the specimens of *D. securis* are essentially indistinguishable from those of the type locality in the middle Cabbage Patch beds (ca. 24 Ma) of the Flint Creek Basin of southwestern Montana. Most specimens are somewhat abraded, the outer chalky layer has been removed, and the growth wrinkles are smoothed, suggesting transport of some distance.

Environment and Distribution.—As with *Deroceras mahiz*.

Material.—Twenty-five specimens. Figured specimen: CM-41663, and additional specimens CM-

41664 (7), KUMIP-289,736 (7), and PLIM-113 (10), all from Kintla Creek-Carnegie (KTL-1) locality, Flathead County, Montana, Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Superfamily Zonitoidea Mörch, 1864

Family Zonitidae Mörch, 1864

Subfamily Zonitinae Mörch, 1864

Genus *Nesovitrea* Cooke, 1921

Type species.—*Vitrea pauxilla* Gould, 1852.

Subgenus *Perpolita* H. B. Baker, 1928

Type species.—*Nesovitrea hammonis* (Ström, 1767).

Nesovitrea pulchra Pierce, 1992

(Fig. 9.Q, 9.R)

Emended description.—Shell strongly depressed, of nearly four regularly increasing whorls, suture scarcely impressed. Embryonic whorls about 1.5, smooth, subsequent whorls with apical sculpture of regular, weak, prosocline growth wrinkles, on some specimens more widely spaced, fine prosocline radial striae appear at about the third whorl, these striae gradually become more prominent and more widely separated, up to 0.5 mm apart just behind aperture, last whorl strongly convex below, base with slightly weaker wrinkle striae. Aperture deeply and obliquely lunate, outer lip retractive about 30° from vertical axis, peristome simple, acute, umbilicus open, initially narrow conical, enlarging with last whorl to become funnel-shaped, contained four to five times in diameter. Measurements of figured hypotype, CMNH 41667: width, major 3.6 mm, minor 2.7 mm; height (estimated, slightly crushed) 1.8 mm; H/W (est.), 0.50; whorls 3.5.

Discussion.—The type specimens from the Cabbage Patch molluscan local fauna of southwest Montana, although plentiful and in good condition, are entirely replaced and recrystallized. The specimens herein from the Kishenehn Basin, although crushed and variously compressed, are composed of original shell material. The finer details of sculpture are revealed, resulting in the emended description, above. As previously concluded, *N. pulchra* appears to be closely related and possibly ancestral to the modern palearctic *N. hammonis* (Ström, 1767) group.

Environment and Distribution.—Palearctic *N. hammonis* is a plausible modern analog of *N. pulchra*. In Kansas, it “is an inhabitant of woodlands where it lives in decaying leaves, beneath loosened bark on dead trees and under sticks and fallen logs, . . . where the annual rainfall is generally more than 35 inches, but it declines in frequency toward the more arid Plains Border, . . . even where timber is locally available” (Leonard, 1950:37). In North America, modern subspecies of this group are found as far south as the 37th parallel (Virginia to Colorado), with probably relic populations in New Mexico and Arizona (Bequaert and Miller, 1973:67, 68, 145). As fossils, *N. hammonis* is known from late Pliocene (Blancan) to Recent faunas (Pierce, 1992:612). *Nesovitrea pulchra* was known previously only from the late Oligocene (early Arikareean) Cabbage Patch fauna of southwestern Montana (Pierce, 1992).

Material.—Forty five specimens. Figured hypotype, CM-41667 is from E-4 (NFF-2) locality, British Columbia. Additional specimens; PZON-104 (2), PZON-105 (14) Commerce Creek (CMC-1) locality; PZON-106 from E-5 (NFF-1) locality; CM-41668 (5) from E-4 (NFF-2) locality, all British Columbia, and KUMIP-289,739, KUMIP-289,740 (6) from Wurtz Bend (NFF-19) locality, Flathead County, Montana. All localities in Lower Member, Kishenehn Formation, late Eocene-Oligocene. Regrettably, several specimens from Kintla Creek-River locality that were examined and listed are now missing. This locality is retained on the Kishenehn Fauna List, Table 2.

Superfamily Polygyroidea Pilsbry, 1895

Family Polygyridae Pilsbry, 1895

Subfamily Polygyrinae Pilsbry, 1895

Genus *Praticolella* von Martens, 1892

Type species.—*Praticolella ampla* (Pfeiffer, 1841).

Praticolella lucifera Pierce, new species

(Fig. 11.M–11.O)

Diagnosis.—Shell small, few whorled, low domed for genus, peristome lightly reinforced and boldly expanded.

Description.—Shell small, glossy pale yellowish brown, low domed depressed helicoid with about 4.2 rounded, regularly expanding whorls, suture moderately impressed, embryonic whorls about 1.5, smooth to very finely punctate, subsequent whorl with fine, regular, slightly prosocline costellae, about 20 per mm, becoming faint and indistinct on remaining whorls; last 0.1 to 0.2 whorl expanding more rapidly, not descending, with four or five faint spiral striae on base of whorl not observed on preceding whorls, aperture ovate lunate, peristome boldly reflected, slightly thickened within, light callus on parietal margin, reflected aperture partially blocking narrow umbilicus. Measurements of holotype: width, major 7.2 mm; width, minor, est. 6.8 mm; height, est. 3.5–4.0 mm, crushed; whorls, 4.2.

Discussion.—*Praticolella lucifera* is remarkably similar to modern *P. griseola* (Pfeiffer, 1841), especially as found on the Mexican Yucatan Peninsula. *Praticolella lucifera* differs in being slightly smaller, having fewer whorls, 4.2 versus 5.0 for *P. griseola*, in having bolder and more regular sculpture on the neanic whorls, and in the more strongly and widely reflected peristome. It is easily separated from *P. berlandierana* (Moricand, 1833) by its greater size, more whorls, and strongly reinforced peristome, and from *P. campi* by its smaller size and weakly reflected peristome. In general, *P. lucifera* shows close affinities to the Section *Praticolella* (*s. str.*) group (*sensu* Thiele, 1992:932), found from Texas to Nicaragua, but is quite distinct from the other section of this species that occurs east of the Mississippi River. *Praticolella prisca* Auffenberg and Portell, 1990, known from the middle Miocene of Florida, is the only other pre-Tertiary occurrence of this genus known.

Environment and Distribution.—*Praticolella griseola*, the closest modern analog, prefers warm, open, or lightly wooded, grassy zones and, although preferring relatively humid conditions, is tolerant to seasonal drought (Pilsbry, 1940:690–695). It is generally distributed from South Texas through eastern Mexico to Nicaragua. Cheatum and Fullington (1971:37) record *P. berlandieriana* as a Pleistocene fossil.

Etymology.—*lucifera*, Latin, shiny.

Material.—Two specimens. Holotype: CM 41669, and CM 41670, a fragment, are from Starvation Bend (NFF-12) locality, Flathead County, Montana, Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Subfamily Triodopsinae Pilsbry, 1940

Genus *Ashmunella* Pilsbry and Cockerell, 1899

Type species.—*Ashmunella rhyssa miorhyssa* (Dall, 1898).

Ashmunella(?) sp.

(Fig. 11.L)

Description.—Shell a slightly depressed helicoid, moderately large for genus, with about five rapidly expanding, rounded whorls, suture moderately impressed, openly umbilicate, ultimate whorl bearing regular, collabral, smoothly rounded ribs spaced at about 0.5 mm intervals, ribs more prominent and stronger on base of whorl; aperture descending moderately in last 3 mm, outer lip well reinforced,

narrowly expanding, rather bluntly terminated, incomplete except for insertion into penultimate whorl which bears a thin callus across parietal region, and a large (~4.5 mm long by 2 mm high), diagonally situated parietal lamella, located well in front of basal lip and partly blocking aperture, with the shallowly sigmoidal apex of the lamella deflected slightly into aperture, outer lip oblique, at 30° angle from the axis. Measurements of holotype (broken and crushed) are as follows: diameter, ~15 mm; height ~8.0 mm; H/W ~0.55; whorls about 5.

Discussion.—Reconstruction is based on a basal fragment which includes more than one-half of the ultimate whorl, with part of the collapsed whorls of the spire in cross section, and a small portion of the inner lip of the aperture, the parietal lamella, and the umbilicus. Had not the parietal lamella been observed, the superficial resemblance of this specimen to *Helminthoglypta* Ancey, 1887 and the known presence of this genus in nearby fossil localities of similar age might have resulted in tentatively placing this species in that genus. However, a combination of factors, i.e., size, shape, ornamentation, aperture, and parietal lamella, surely places this species in the Polygyridae, and, most likely, in the Triodopsinae. The shells of the genera of the Triodopsinae are rather similar, and the placement of this specimen in a genus is somewhat questionable. This specimen seems to combine conchological traits of the modern genera *Ashmunella*, *Vespericola* Pilsbry, 1939, and the subgenus *Cryptomastix* Pilsbry, 1939 of *Triodopsis* Rafinesque, 1819. All of these share many conchological characters in common, but each can be distinguished by unique characters that are often difficult to distinguish. This species has the strong, robust parietal lamella characteristic of *Cryptomastix*, the somewhat heavier shell of *Vespericola*, and the open umbilicus of *Ashmunella*, and the strong sculpturing of the ultimate whorl not noted among the *Cryptomastix* or the *Vespericola*. In fact, this species would make a good progenitor for the western polygyrids. Based on the openly umbilicate nature of this specimen, which is probably a primitive character, the strong sculpture of the ultimate whorl, and the interpreted environment in which encountered, it appears more closely related to the genus *Ashmunella*, and is so assigned herein, but with question. Among extant members of the genus, the sculpture of *Ashmunella*(?) sp. resembles that encountered among the subspecies of *A. townsendi* Bartsch, 1904.

Environment and Distribution.—Modern distribution is limited to far West Texas, southwestern New Mexico, southeastern Arizona, and northern Chihuahua. “Most species live at moderate elevations (4,000–6,000 feet), but a few reach 9,000–12,000 feet (e.g. in New Mexico). They prefer well-sheltered and shaded biotopes in sloping talus of loose soil and rock debris” (Bequaert and Miller, 1973:37). Fossil occurrences of the genus prior to the Pleistocene have not been reported (Bequaert and Miller, 1973:40).

Material.—One specimen. Illustrated type CM 41671 is from Commerce Creek (CMC-1) locality, British Columbia, Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Superfamily Camenoidea Pilsbry, 1895

Family Oreohelicidae Pilsbry, 1939

Genus *Oreohelix* Pilsbry, 1903

Type species.—*Helix strigosa* Gould, 1846.

Discussion.—The generally accepted conchological differences between the modern genera *Oreohelix* and *Radiocentrum* Pilsbry, 1905, have been defined by Pilsbry (1939:418) as follows: “Embryonic shell of one and one half radially costulate whorls . . . Subgenus *Radiocentrum*; Embryonic shell of more than two whorls at birth, variously wrinkled and striate . . . Subgenus *Oreohelix s. str.*” On

the same page, in his Key to Species of *Oreohelix*, he altered these definitions as follows: "Embryonic shell strongly ribbed radially, of about $1\frac{1}{2}$ whorls . . . Subgenus *Radiocentrum*; Embryonic shell of about $2\frac{1}{2}$ whorls, which are striate and usually with spiral lines . . . Subgenus *Oreohelix s. str.*" Although the definition of *Radiocentrum*, i.e., embryonic shell of one and one-half whorls and strongly ribbed, can be applied to fossil Oreohelicidae without modification, the criteria for *Oreohelix* essentially denies fossil existence of the genus. Nearly all fossil Oreohelicidae have been reclassified as *Radiocentrum* (Roth, 1986; Taylor, 1975). I know of no fossil oreohelicid with a protoconch of two or more whorls. Considering modern distributional patterns, it is unlikely that the genus *Oreohelix* is a modern derivative of the genus *Radiocentrum*, although ancient derivation is plausible. Therefore, to be of any value in defining fossil taxa, the Pilsbry definition of *Oreohelix* (above as subgenus) must be altered to admit those taxa with a weakly ornamented (striate? or weakly costulate) protoconch of one and three-quarters or more whorls, and such definition is used herein.

Oreohelix dawsonae Pierce, **new species**
(Fig. 12.A–12.D)

Diagnosis.—A strongly depressed heliciform shell, openly umbilicate, about 5.5 costate whorls, sharply angular at shoulder of juvenile whorls, becoming rounded in last whorl, aperture simple, strengthened within, basal lip weakly reflected.

Description.—Shell moderately large, strongly depressed heliciform to sub-lenticular, of 5.5 or more modestly rounded whorls, suture shallowly impressed, openly umbilicate. Embryonic whorls about 1.75, initial $\frac{5}{8}$ whorl smooth to finely granulose, second $\frac{5}{8}$ whorl with weak but regular wrinkle costulae, final $\frac{1}{2}$ whorl with regular, but weak, costulae, becoming less regular, prosocline costae on neanic whorls; whorls initially strongly angular at shoulder, becoming rounded in last whorl, descending in last few millimeters behind aperture. Aperture rounded, lip simple, blunt, oblique, strengthened within, columellar margin reflected around umbilicus, basal margin very weakly reflected. Measurements of holotype: height (est.) 8.0 mm, crushed; width 15.9 mm; H/W (est.) 0.50; whorls >5.5 .

Discussion.—The clear-cut distinction between the genera *Oreohelix* and *Radiocentrum* as proposed by Pilsbry (1939:418) appears blurred when dealing with mid-Tertiary species. Fossil *Oreohelix* are rare. Late Oligocene *Oreohelix brandi* Pierce, 1992, from the Cabbage Patch fauna of southwest Montana, has two or fewer, usually about 1.75, embryonic whorls, is initially smooth for first one-half whorl, then weakly costulate (Pierce, 1992:616). Roth (1986:249–252) has described two new species of the Oreohelicidae, as genus *Radiocentrum*, from Eocene to early Oligocene strata in the Three Forks Basin of west central Montana. *Radiocentrum taylori* Roth, 1986, has a "Protoconch consisting of 1.5 whorls, nuclear tip smooth, thereafter with prominent, elevated radial ribs . . ." Detail of the apical (protoconch) sculpture (Roth, 1986:fig. 20) clearly verifies that this is, according to the criteria established by Pilsbry (loc. cit.) a *Radiocentrum*. On the other hand, "*Radiocentrum laevidomus* Roth, 1986, has a "Protoconch of 1.75 whorls, nuclear tip smooth, followed by smooth, regular, forwardly convex radial ribs . . ." Examination of Roth's (1986:fig. 30) excellent photograph of Paratype USNM 377388, a hatchling young of *R. laevidomus*, shows that the smooth nuclear tip is about 0.75 whorl, followed by weak but regularly spaced costulae (wrinkles?) for the remainder of the embryonic whorls. The weak sculpture and extended protoconch (1.75 whorls) meet the criteria established above for the genus *Oreohelix*, and compares very closely with the character of embry-

onic whorls of both *Oreohelix brandi* and *Oreohelix dawsonae*. From this, it would appear that "*Radiocentrum*" *laevidomus* is best considered an *Oreohelix*.

Oreohelix dawsonae is quite similar to *O. laevidomus*, but differs in being larger, and in having an even more depressed spire (H/W est. 0.50 versus H/W 0.55 to 0.63 for *O. laevidomus*). *Oreohelix brandi*, although about the same size, has a much more elevated spire (H/W ~0.77). *Oreohelix leonti* (Stearns, 1902) (holotype not seen), from the John Day Miocene of Oregon, is the only other fossil member of this genus. It differs in being smaller, having a somewhat more elevated spire, H/W ~0.55, and fewer whorls that are "closely and conspicuously ribbed" (Stearns, 1902:154).

Environment and Distribution.—An intermontane genus, widely distributed from Alberta and British Columbia to New Mexico, Arizona and Nevada, but generally north of the area occupied by *Radiocentrum*. They are generally found on limestone slopes and talus. In the northern part of their range they are found in well-wooded environments near streams and at low altitudes, and usually occupy sparsely vegetated higher altitudes near their southern limits (Pilsbry, 1939: 412–540; Baquaert and Miller, 1973:32–37.) The earliest fossil *Oreohelix* are late Eocene-Oligocene *O. laevidomus* from the Three Forks Basin of west central Montana and Oligocene to early Miocene *O. brandi* from the Cabbage Patch fauna of southwestern Montana.

Etymology.—Named to honor Dr. Mary Dawson, paleontologist, friend, and Curator of Vertebrate Paleontology, Carnegie Museum of Natural History, with whom I have spent many pleasant hours collecting fossils in the Kishenehn Basin.

Material.—Seven specimens. Holotype CM-41624 and paratypes KUMIP-289,708 and KUMIP-289,709 are from E-5 (NFF-1) locality, British Columbia, Kishenehn Formation, middle Eocene-late Oligocene. Additional paratypes are: CM-41625 from Commerce Creek (CMC-1) locality, British Columbia and PORH-111 (3 fragments) from Kintla Creek River (NFF-17) locality, Flathead County, Montana, all from Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Genus *Radiocentrum* Pilsbry, 1905

Type species.—*Oreohelix chiricahuana* Pilsbry, 1905.

Radiocentrum kintlana Pierce, **new species**

(Fig. 12.E–12.G)

Diagnosis.—A moderate-sized, strongly depressed trochoidal shell with regularly spaced costae crossed by weak, discontinuous, spiral striae above periphery on ultimate whorl, strongly shoulder carinate in early whorls, more roundly keeled in last half whorl.

Description.—Shell strongly depressed trochoid, of about 4.5 to 5.0 slightly rounded, sharply shoulder carinate whorls that become more roundly keeled on last half of ultimate whorl, suture lightly impressed, openly umbilicate. Embryonic whorls about 1.5, with smooth nuclear tip preceding fine but strong, evenly spaced, prosocline costulae, subsequent whorls bearing coarser, regularly and closely spaced costae, with six discontinuous weak spiral striae crossing and cutting the costae into long granules above the periphery on the ultimate whorl. Aperture sub-lunate, simple, lip thin but blunt, not thickened within, not reflected. Measurements of holotype: height (est.) ~7.0 mm (crushed); width 14.5 mm; H/W (est.) 0.48; whorls >4.5.

Discussion.—The holotype, CM 41626, is fragmented, lacks the embryonic whorls and the palatal portion of the aperture. The paratype, CM 41627, is slightly crushed and incomplete, retaining only ~4 whorls, but with good embryonic whorls. There is no hesitation in placing these specimens in the genus *Radiocentrum*. Among modern members of this genus, *Radiocentrum avalonense* "Hemphill" Pilsbry, 1905 is quite close, differing in having stronger embryonic cos-

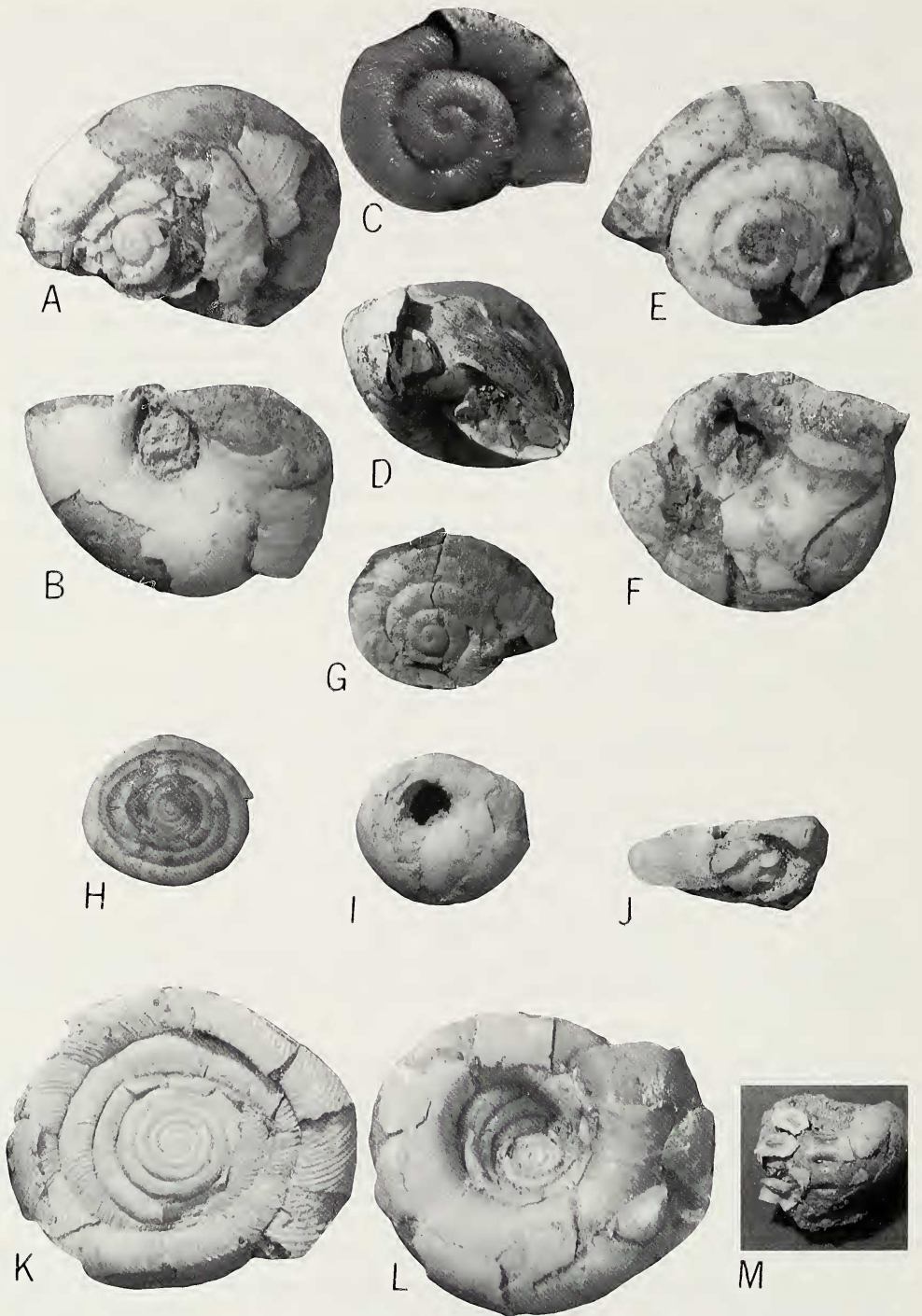


Fig. 12.—STYLOMMATOPHORA: OREOHELICIDAE. A–D: *Oreohelix dawsonae* n. sp. A–C: Holotype (CM 41624); A, apical, X3; B, umbilical, X3; C, nuclear whorls, enlarged, X12; D, Paratype (KUMIP 289709), X3, compressed aperture; E–F: *Radiocentrum kintlaense* n. sp. Holotype (CM

tulae, stronger and more closely spaced rough, irregular, costae, and in having spiral striae on the base only. Among fossil members of this genus that are similar, late Cretaceous *Radiocentrum anguliferum* (Whiteaves, 1885) is almost flat dorsally, and Eocene *R. grangeri* (Cockerell and Henderson, 1912) is much larger, and both have a more angular periphery on the body whorl. Paleocene *Radiocentrum thurstoni* (Russell, 1926), early Oligocene *Radiocentrum taylori* Roth, 1986, and Oligocene *Radiocentrum hendersoni* (Russell, 1938) all have higher, more dome-like spires than *R. kintlana*.

Environment and Distribution.—A calciphilic genus, usually found in isolated mountain top colonies, on talus slopes, rockfalls, and/or near water usually above 5,000 feet. Isolation and dispersion of species suggests relic populations representing a previously more widespread distribution. Several species are known only from dead shells (Pilsbry, 1939:540–553). The genus is found living only in southern New Mexico and Arizona, northwestern Chihuahua, Baja California Sur, and, with a single species, Santa Catalina Island, California (Roth, 1986:248; Hochberg et al., 1987). Fossil species are not uncommon, ranging from Cretaceous *R. angulifera* (Whiteaves, 1885) and Paleocene *R. thurstoni* (Russell, 1926) of western Alberta, through several mid-Tertiary taxa of the intermontane West. *Radiocentrum taylori* Roth, 1986, from the late Eocene to early Oligocene of the nearby Three Forks Basin of west central Montana, is temporally and geographically close.

Etymology.—Named in reference to the Lower Kintla Rapids locality where this species was found.

Material.—Two specimens. Holotype, CM-41626, and paratype, CM-41627, are from Lower Kintla Rapids (NFF-18) locality, Flathead County, Montana, Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Family Megomphycidae Baker, 1930b

Genus *Polygyroidea* Pilsbry, 1923

Type species.—*Daedalochila harfordiana* Cooper, 1870.

Polygyroidea montivaga Pierce, 1992

(Fig. 12.H–12.J)

Discussion.—This species, so commonly encountered in the late Oligocene to early Miocene Cabbage Patch molluscan local fauna of the intermontane basins near Drummond, Montana, was rather rarely encountered at only two localities. One specimen, KUMIP 289741, from the CMC-1 locality, was complete enough to retain the distinctive parietal lamella (Fig. 11.J), so there can be no doubt as to identification. The remaining specimens were separated from the more common *Polygyrella*, cf. *P. polygyrella* (Bland and Cooper, 1861) on the basis of shape, *P. montivaga* is thicker (H/W greater), and on the character of the basal portion of the later whorls, e.g., *P. montivaga* whorls are smoother on the base, whereas those of *P.*, cf. *P. polygyrella* are lightly wrinkled. Pilsbry (1939:554–555) notes

←
41626), X3; E. apical; F. umbilical; G. *R. kintlai* (CM 41627) X3, apical. MEGOMPHICIDAE. H–I. *Polygyroidea montivaga* Pierce, 1992 Hypotype (CM 41672), X3; H. apical; I. umbilical; J. *P. montivaga* Hypotype (KUMIP 289741) X3, apertural, showing parietal lamella; K–M: *Polygyrella polygyrella* (Bland and Cooper, 1863) K–L: Hypotype (CM 41674), X3; K. apical; L. umbilical; M. *P. polygyrella* Hypotype (PAMM-109), X2, radial teeth folded back showing casts of teeth in body whorl in-filling.

that "There are indications that the Ammonitellinae are a very old group, for a long time declining, some genera now perhaps approaching extinction. All of the genera except *Glyptostoma* are monotypic, and the ranges of the species are narrowly limited, . . . characteristics of decadent groups." Measurements of hypotype: width 8.4 mm; height 4.7 mm; H/W 0.56; whorls >7.25.

Environment and Distribution.—This currently monotypic genus, *P. harfordiana*, is found living only in Fresno and Mariposa Counties of California in Transition Zone forests generally above 1,800 m altitude (one colony at 1,220 m), where the Mean Annual Temperature (MAT) is about 10°C and the Mean Annual Precipitation (MAP) is probably >100 cm (Pierce, 1993:989). The only other fossil occurrence of *P. montivaga* is the late Oligocene to early Miocene Cabbage Patch fauna of southwestern Montana (Pierce, 1992). Roth (in press) describes a new species from the Cretaceous (Campanian) of California. Photographs furnished by Roth (1999) leave no doubt as to its generic identity. Pilsbry's comments, above, are certainly substantiated.

Material.—Nine specimens. Figured specimen CM 41672, KUMIP-289,742 (2), and PAMM-108 are from Wurtz Bend (NFF-19) locality, Flathead County, Montana. Figured specimen KUMIP 289,741, CM-41673 (2), and PAMM-107 (2) are from Commerce Creek (CMC-1) locality, British Columbia. Both localities are in the Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Genus *Polygyrella* Bland and Cooper, 1861

Type species.—*Helix polygyrella* Bland and Cooper, 1861.

Polygyrella sp., cf. *P. polygyrella* (Bland and Cooper, 1861)
(Fig. 12.K–12.M)

Polygyrella sp., cf. *P. polygyrella*, B. Roth, 1986:253, figs. 31,32.

Polygyrella polygyrella, G. D. Hanna, 1920a:3.

Polygyrella indet., D. W. Taylor in C. P. Ross, 1959:71.

Zonitoides? sp., L. S. Russell, 1956a:110,111, pl.1, fig 8.

Description.—"Shell subdiscoidal with broad umbilicus contained approximately three times in diameter. Spire flat to low-convex, suture lightly impressed. Whorls tightly coiled, sometimes with closely spaced, forwardly convex radial grooves extending outward from suture, not reaching shoulder of whorl. Body whorl with up to four shallow transverse constrictions. Last whorl not markedly descending except immediately behind aperture. Aperture oblique, peristome thickened and slightly expanded outward" (Roth, 1986:253). Within the last whorl there are one or more radial rows of three teeth each.

Discussion.—Referring to this taxon as *P. sp.*, cf. *P. polygyrella* merely signifies that, conchologically, the material at hand cannot be distinguished from the normal range of variation of shells of modern *P. polygyrella*. There is no connotation that they are the same species, which is considered highly unlikely. Even minimal genetic drift, considering the years involved, would insure specific separation. The shell material of these specimens is, essentially, original. Although the radial teeth are not visible through the shell, as with modern specimens, many of the fragmented specimens either have these radial teeth on detached shell fragments, or as molds on exfoliated cores. Figure 12.M (PAMM-109, Lower Kintla Rapids, NFF-18) is of a section of a whorl displaying as molds the arrangement of the three radial teeth, with each tooth laid back alongside its mold for comparison. One specimen has a crushed but essentially complete aperture (PAMM-108, NFF-1), which confirms Roth's description, above. Neither Roth (1986:253), nor the author, were able to find any evidence of the large parietal tooth so characteristic of the modern species. Considering the number of specimens stud-

ied, by both Roth and the author, it appears most likely that this mid-Tertiary polygyrellid is without a parietal tooth, and is, therefore, specifically distinct from the modern species. That it also is found in the Three Forks l.f. and the White River l.f. suggests adaptation to a climate drier and warmer than the modern species lends some support to this theory. Better specimens are needed to confirm this.

Russell (1956:110, 111, pl. 1, fig. 8), working with very limited and incomplete material from a single locality, E-2, considered apical fragments of *P. sp.*, cf., *P. polygyrella* to be *Zonitoides?* sp. A very limited collection was made from or near his E-2 locality, without finding any specimens referable to this species.

Environment and Distribution.—*Polygyrella* is now a monotypic genus whose current range is limited to northern Idaho, Montana, and northeastern Washington, where it is found in damp spruce forest and on lava and schist talus (Pilsbry, 1939:559). As a fossil, the genus has been reported from strata as old as Cretaceous, [*P. parvula* (Whiteaves, 1885), and *P. amplexus* (Meek and Hayden, 1857)] and as *P. sp.*, cf. *P. polygyrella* from the Eocene by Roth (1986:253), and from the Miocene by Hanna (1920a:3). I can find no reference to *P. polygyrella* as a Recent or Pleistocene fossil.

Material.—More than sixty specimens. Figured Specimens are as follows: CM 41674 from Starvation Bend (NFF-12) locality, and PAMM 109 from the Lower Kintla Rapids (NFF18) locality, both Flathead County, Montana. Additional specimens are as follows: PAMM 110 and 111 from Commerce Creek (CMC-1) locality (16); PAMM 112 and PAMM 117 from E-5 (NFF-1) locality (14), both British Columbia; KUMIP 289,744 (4) and PAMM 113 (9) from Starvation Bend (NFF-12) locality; PAMM 115 from Kintla Creek-River (NFF-17) locality (3); KUMIP 289,743 (1) and PAMM 114 (3) from Lower Kintla Rapids (NFF-18) locality; CM 41675 (8) and PAMM 116 (3) from Wurtz Bend (NFF-19) locality, all Flathead County, Montana. All localities are in the Lower Member, Kishenehn Formation, lower Eocene-Oligocene.

Superfamily Helicoidea Rafinesque, 1815
Family Humboldtianidae Pilsbry, 1939
Genus *Skinnerelix* Evanoff and Roth, 1992

Type species.—*Helix leidy* Hall and Meek, 1855.

Diagnosis.—“Shell large (adult shells larger than 2 cm in maximum diameter); globose-conic; height to maximum diameter ratio greater than 0.8; embryonic shell smooth, consisting of first 1.2 whorls; neanic sculpture of growth rugae and coarse, somewhat crude granulation arranged in diagonal rows; last whorl broadly rounded, tumid, descending, constricted basally just behind lip; peristome flaring, narrowly turned outward, reflected at base and columella; base narrowly, obliquely perforate” (Evanoff and Roth 1992:124).

Environment and Distribution.—*Humboldtiana* von Ihering, 1892 “is a plausible environmental analog to *Skinnerelix* . . . ranges from Mexico City, Mexico, north to the Guadeloupe Mountains in southeast New Mexico . . . It typically lives in a variety of substrates and woody vegetation, ranging from oak forest on limestone to high coniferous forests and mixed scattered woodlands on volcanic rocks (Pilsbry, 1939). The climate in the range of *Humboldtiana* is subtropical . . . with mean annual range of temperatures of 4–20°C . . .” (Evanoff and Roth, 1992:129). Fossil *Skinnerelix leidy* are known from the late Eocene and early Oligocene (Chadronian and Orellan Land Mammal Ages) of Nebraska, South Dakota, Utah and Wyoming (Evanoff and Roth, 1992:fig. 8).

Skinnerelix rothi Pierce, **new species**
(Fig. 13.A–13.C)

Diagnosis.—Shell large, openly umbilicate, nuclear whorls smooth to finely pitted, sculpture of rough collabral costae broken into irregularly elongate, flat-topped granules, body whorl bears incised, spiral lines below and parallel to suture.

Description.—Shell large, globose-conic, openly umbilicate, with about 4.75 rapidly expanding whorls; spire broadly convex, nuclear diameter 0.65 mm, embryonic whorls 1.5 to 1.75, smooth to finely pitted, flatly rounded, suture modestly impressed, indistinctly separated from subsequent whorls initially bearing closely spaced, irregular, collabral costellae which gradually become rough collabral costae generally broken into irregularly elongate, flat-topped granules aligned along costae; body whorl with indistinct, incised, spiral lines below and parallel to suture, last $\frac{1}{8}$ whorl behind aperture descends rather abruptly; aperture lunate-ovate, outer lip thickened and narrowly reflected, basal and columellar becoming recurved. Measurements, estimated, of compressed holotype: height 19 mm; width 24 mm; H/W 0.79; height of aperture 13 mm; width of aperture 14 mm; whorls 4.75.

Discussion.—*Skinnerelix rothi* is obviously very similar to *S. leidyi*, from which it is not easily separated. The chief differences in *S. rothi* are a slightly more depressed shape, an open umbilicus, incised, spiral lines parallel to the suture on the ultimate whorl, and costae broken into irregularly elongate, flat-topped granules on the ultimate whorls, which are quite different from the fine, diagonally arranged, collabral granulations of *S. leidyi*. *Skinnerelix rothi*, as well as *S. leidyi*, can be quickly distinguished from various species of the genus *Humboldtiana* von Ihering, 1892 by the thickened, reflected, and recurved lip typical of *Skinnerelix*. Roth (1999, personal communication) kindly examined these, and other large gastropods from this fauna, and his keen observations and comments are reflected in the Description above.

Etymology.—*rothi*, in honor of Barry Roth, University of California, Berkeley, Museum of Paleontology, and Editor of *The Veliger*, a preeminent molluscan paleontologist.

Material.—More than thirty-six specimens, all incomplete, badly compressed and/or crushed and fragmented. The holotype, figured specimen CM 41676, is from Starvation Bend (NFF12) locality, Flathead County, Montana, Kishenehn Formation, Coal Creek member, late Oligocene. Additional specimens: Paratypes CM 41677 (6), KUMIP 289,745, KUMIP 289,746 (6), and PHBD 101–105(23) are from Starvation Bend (NFF-12) locality, PHBD-106 is from Moose City South (NFF-10) locality, and PHBD 107 (3 apical fragments) is from Lower Kintla Rapids (NFF-18) locality, all Flathead County, Montana, Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Superfamily Xanthonychoidea Strebel and Pfeiffer, 1880

Family Helminthoglyptidae Pilsbry, 1939

Genus *Xerarionta* Pilsbry, 1913

Type species.—*Arionta veatchii* Tryon, 1866, *ex* Newcomb MS.

Xerarionta constenii Pierce, **new species**

(Fig. 13.D–13.F)

Diagnosis.—Shell moderately large, depressed globose, obliquely umbilicate, aperture roundly lunate, sculpture of embryonic whorls smooth to finely granular, subsequent whorls with collabral costellae that become rugae extending from suture to umbilicus on ultimate whorls.

Description.—Shell moderately large, depressed globose, spire convex, apical angle about 130°, umbilicus obliquely open, nuclear diameter 0.65 mm, embryonic whorls about 1.5, smooth to very finely granular, neanic whorls bear weak, closely spaced, collabral costellae becoming irregularly spaced rugae that continue over periphery into umbilicus on ultimate whorl, aperture roundly lunate, scarcely descending, outer and basal lips missing, columellar lip thin, broadly recurved around um-

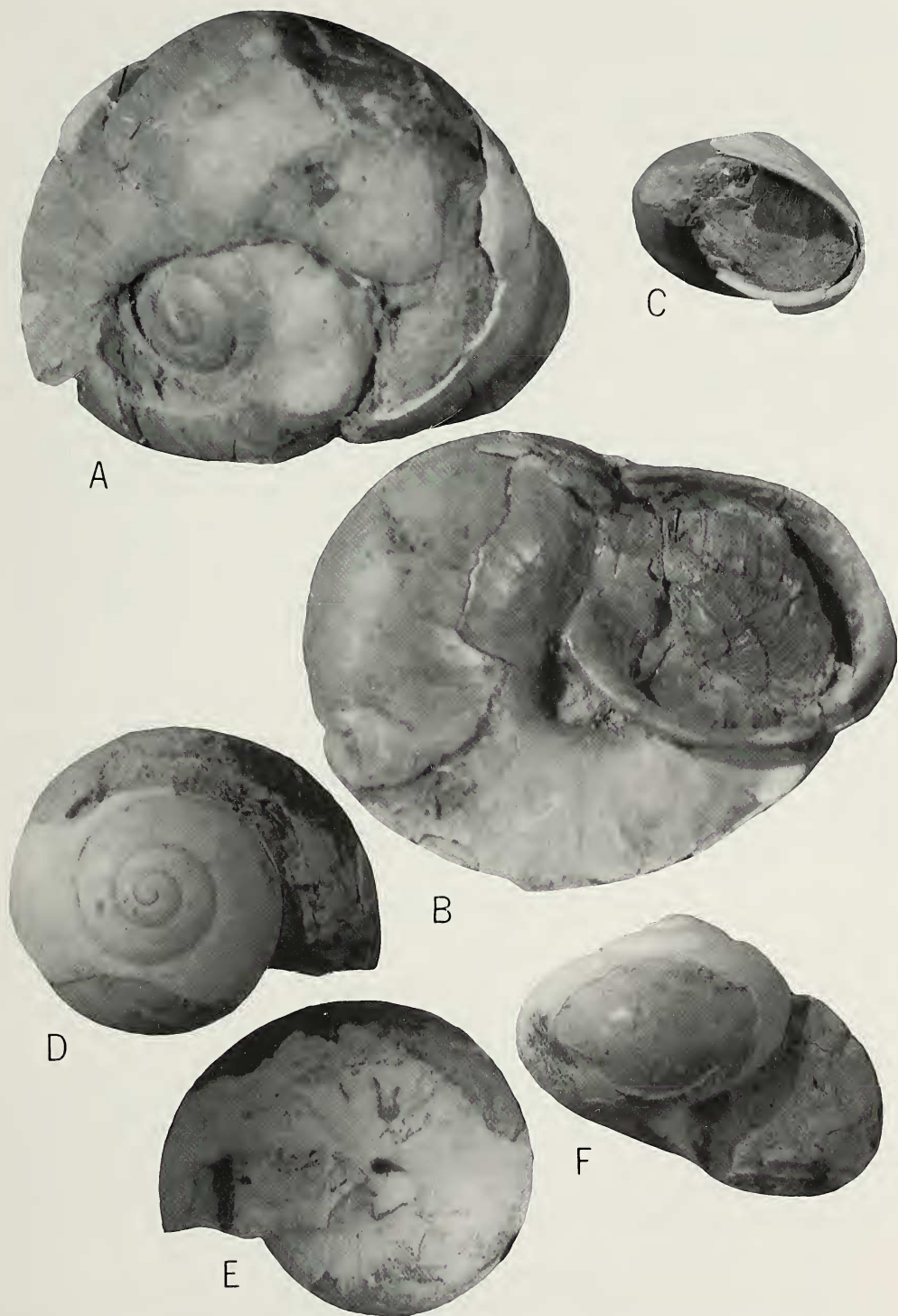


Fig. 13.—STYLOMMATOPHORA: HUMBOLDTIANIDAE. A–C: *Skinnerelix rothi* n. sp. A–B: Holotype (CM 41676), X3; A. apical; B. umbilical, note *Anguispira* sp., cf. *A. alternata* wedged in aperture; C. *Skinnerelix rothi* Paratype (PHBD-102), X1.7, detached aperture, frontal view. HELMINTHOGLYPTIDAE. D–F: *Xerarionta constenii* n. sp. Holotype (CM 41678), X3; D. apical; E. umbilical; F. apertural.

bilicus. Measurements of holotype: width, major 18.2 mm; width, minor 15.1 mm; height 14.3 mm; H/W 0.79; width of aperture 10 mm; height of aperture 10 mm; whorls >4.2.

Discussion.—Roth (personal communication) examined the holotype and concluded that this specimen is immature. The few whorls of the holotype are in agreement with this conclusion. Roth further compared the holotype to living *X. redimita* (W. G. Binney, 1858), from San Clemente Island, and found similarities in shape, but differences in sculpture. Fossil *Helminthoglypta bozemanensis* Roth, 1986, from the nearby late Eocene-early Oligocene Three Forks Basin is grossly similar but is smaller and has a more elevated spire. Fossil *Xerarionta* are not well known. Late Eocene (Uintan-Chadronian) *Xerarionta waltmilleri* Roth, 1984, is quite similar to *X. constenii*, especially in surface sculpture, but is much larger. Evanoff and Roth have another, yet undescribed, *Xerarionta* from latest Chadronian and/or early Orellan White River strata near Douglas, Wyoming. The two species can be discriminated by the difference in dimensions of the nuclear whorls (Roth, 1997, personal communication).

Environment and Distribution.—Roth (1984:214) found that “*Xerarionata* now occurs on the southern California Channel Islands and the adjacent mainland, and along the western part of Baja California between latitudes 24°–31°N. The Baja California occurrences are all within the arid, subtropical to tropical Sonoran Desert.” Roth (op. cit.) further determined the climatic conditions of known population localities ranged from MAT of 17°–21.5°C with mean annual ranges of temperature from 7.2°–10°C, and generally are within areas influenced by the Pacific fog. Geologic range of the genus includes late Eocene to early Oligocene (Uintan-Orellan).

Etymology.—Named to honor Kurt Constenius, geologist, friend and driving force behind this multidisciplinary study of the Kishenehn Basin.

Material.—Thirteen specimens. Holotype: CM 41678, is from Bowman Creek (BWN-2) locality, and paratypes: CM 41679 (2); KUMIP 289747; KUMIP 289748 (2); PHLM-101; PHLM-102 (3); and PHLM-105 are from Starvation Bend (NFF-12) locality, both Flathead County, Montana. Additional paratypes: PHLM-103 (4 apical fragments) is from E-2 (NFF-6) locality; and PHLM 104 (4 apical fragments) is from E-4 (NFF-2) locality, both British Columbia. All localities in the Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Aquatic Taxa

Order Mesogastropoda

Superfamily Risssoidea Gray, 1847

Family Hydrobiidae Troschel, 1857

Discussion.—The Hydrobiidae are among the many freshwater snail families wherein even generic identification on the basis of shell features alone is risky. As Taylor (1975:379) so aptly stated, “Classification of Hydrobiidae is based mainly on features of the operculum and reproductive system, for shells of these snails are generally without distinctive features.” Although it is believed that assignment to subfamilies herein is correct, generic assignments are less certain.

Subfamily Hydrobiinae *s. str.*

Genus *Tryonia* Stimpson, 1865

Description.—“Shell perforate, elongated, turreted, subulate, acute at summit and rather pointed at base; surface longitudinally ribbed or plicated, not spinous; whorls numerous, shouldered. Aperture

small, oblique, rhombo-ovate; and somewhat pointed, sinuated and effuse at base; outer lip thin and sharp, projecting below; inner lip appressed to the whorl above, peritreme however continuous" (Stimpson, op. cit.).

Type species.—*Tryonia clathrata* Stimpson, 1865.

Tryonia russelli Pierce, **new species**

(Fig. 14.F–14.H)

Goniobasis sp. Russell, 1952:125, 132, pl. 19, fig. 14–17; 1956:105.

Diagnosis.—Shell small, slender, with strongly rounded whorls, blunt apex, very weak spiral striae and collabral growth wrinkles becoming rugae on last whorls.

Description.—Shell large for *Tryonia*, thin, minutely perforate, very slender, whorls slowly and regularly enlarging, about 20°, from an obtuse apex; nucleus flat or scarcely projecting, first two whorls smooth, subsequent whorls with irregular collabral growth wrinkles becoming noticeably costate on ultimate whorls, all whorls well rounded, suture deeply impressed; aperture ovate-lunate, simple, thin, reflected over columellar margin. Measurement of holotype: height, estimated about 9.0 mm; width, 2.7 mm; H/W 3.33; height of aperture, 2.6 mm; width of aperture, 1.7 mm; whorls estimated 7.0.

Discussion.—Had Russell (1952:132) seen a more complete specimen, he would have realized that this little snail is a hydrobiid, not a pleurocerid. The thinness of the shell, the height and inflation of the whorls, and the blunt apex all confirm this. Among the seven species of this genus previously known (Leonard and Franzen, 1946), the most strikingly similar are *T. hibbardi* Leonard and Franzen, 1944, from the early Pliocene Laverne Formation of northwestern Oklahoma, and *T. ellipsostoma* Pilsbry 1934a; 1934b, from the early Pliocene Tulare Formation of the Kettleman Hills, California. *Tryonia russelli* differs markedly from both in size. However, the three species appear to be closely related and to form a natural group, with *T. russelli* the largest species of this group, as well as the oldest.

Etymology.—Named to honor the late Dr. Loris S. Russell, Royal Ontario Museum, who first encountered this species during his pioneering work in this valley.

Environment and Distribution.—Pilsbry (1934a:542) interpreted the type locality of *Tryonia ellipsostoma* (Kettleman Hills, California) to have been a large, shallow lake with abundant aquatic flora. Leonard and Franzen (1944:34), after an extensive review of the total Laverne fauna (Beaver County, Oklahoma), reached a quite similar conclusion, either a large, shallow, well-vegetated lake, "or more probably, a series of small lakes or ponds in a large basinal area and fed by freshwater streams." Both are of early Pliocene age.

Material.—Four nearly complete specimens, variously crushed, and six detached apical segments of 2–3 whorls each. Holotype, CM 41680, and paratypes CM 41681, KUMIP 289,749 and KUMIP 289,750, are from W-2 (NFF-5) locality, British Columbia, Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Subfamily Nymphophilinae Taylor, 1966

Genus *Cincinnatia*? Pilsbry, 1891

Type species.—*Paludina integra* Say, 1821.

Cincinnatia? *bowmanana* Pierce, **new species**

(Fig. 14.D, 14.E)

Diagnosis.—A small, straight-sided conical shell of about 5.5 whorls, with tiny nucleus elevated above subsequent whorl.

Description.—A small, conical shell, apical angle about 55° , of more than 5.5 well rounded, regularly expanding whorls; nucleus tiny, about 0.20 mm in diameter, elevated above second whorl, apex acutely rounded, embryonic whorls about 1.5, finely punctate, with very weak collabral wrinkles after second whorl, strongest on body whorl; umbilicus tiny, chink-like, aperture ovate, a little more than one-third of shell height, acutely angular at parietal insertion, adnate to body whorl, basal and outer lip simple and sharp, columellar margin slightly flared. Measurement of holotype: height, 4.1 mm; width, 2.55 mm; W/H 0.62; height aperture: 1.5 mm; width aperture, 1.3 mm; whorls 5.7.

Discussion.—Provisional placement of this species in the genus *Cincinnatia*, which is generally of eastern distribution, rather than the closely allied and conchologically almost identical genus *Pyrgulopsis* Call and Pilsbry, 1886, which is mostly western in distribution, is based on the projecting nucleus and acutely rounded apex of this species. *Cincinnatia cincinnatiensis* (Anthony, 1840), which most closely resembles this new species, is distributed as far west as Utah (Clarke, 1973:242). *Cincinnatia cincinnatiensis* can be distinguished from *C?. bowmanana* by its less acute (70°), convexly conical spire and slightly taller aperture. Although several fossil species resemble *C?. bowmanana*, they can be differentiated by the unique combination of characters possessed by *C?. bowmanana*, i.e., projecting nucleus, acutely rounded apex, straight-sided conical shape, apertural character and tiny, chink-like umbilicus. Among those with generally similar appearance are Cretaceous *Hydrobia subconica* Meek, 1876, Eocene *H. anthonyi* (Meek and Hayden, 1856), and *Melania simpsoni* (Meek, 1860), Pliocene *Amnicola bithnoides* Yen, 1944, and Pleistocene to Recent *Pyrgulopsis longinqua* (Gould, 1855). *Cincinnatia? bowmanana* does not appear to be the "*Goniobasis*" sp. collected by Russell (1952:132) from his locality W-1. Russell's material was fragmentary and of too poor quality to describe in detail, however it seems to be a more elongate species, with an apical angle of $\sim 35^\circ$ (Russell, 1952:132, pl. 19, figs. 14–16).

Etymology.—Named for the type locality, Bowman Creek, a tributary of the North Fork of the Flathead River in Flathead County, Montana.

Environment and Distribution.—*Cincinnatia cincinnatiensis*, which may be a close, living analog, is a denizen of diverse habitats ranging from large lakes to small rivers, in general shallow, but well vegetated, water and over bottoms ranging from mud to sand. The species is widely distributed, from New York to southern Saskatchewan and south to Utah and Texas (Clarke, 1973:242). The geologic range of *Cincinnatia* is Pleistocene to Recent, and for the companion genus, *Fonticella*, Gregg and Taylor, 1965, early to middle Pliocene to Recent.

Material.—Two specimens. Holotype, CM 41682, a complete shell with some apertural breakage, and paratype CM 41683, an apical fragment of three whorls, and a smaller fragment, are from Bowman Creek (BWN-2) locality, Flathead County, Montana, Lower Member, Kishenehn Formation, early Eocene-Oligocene. The matrix mold of the back of the holotype is retained as PHDB-101.

Subfamily Lithoglyphinae Hartmann, 1821

Genus *Fluminicola* Stimpson, 1865

Type species.—*Paludina virens* Lea, 1838.

Fluminicola? calderense Pierce, **new species**

(Fig. 14.A–14.C)

Diagnosis.—A small, bluntly conical shell with small, non-protruding nucleus, large, subrectangular aperture with columellar margin expanded over and around umbilicus.

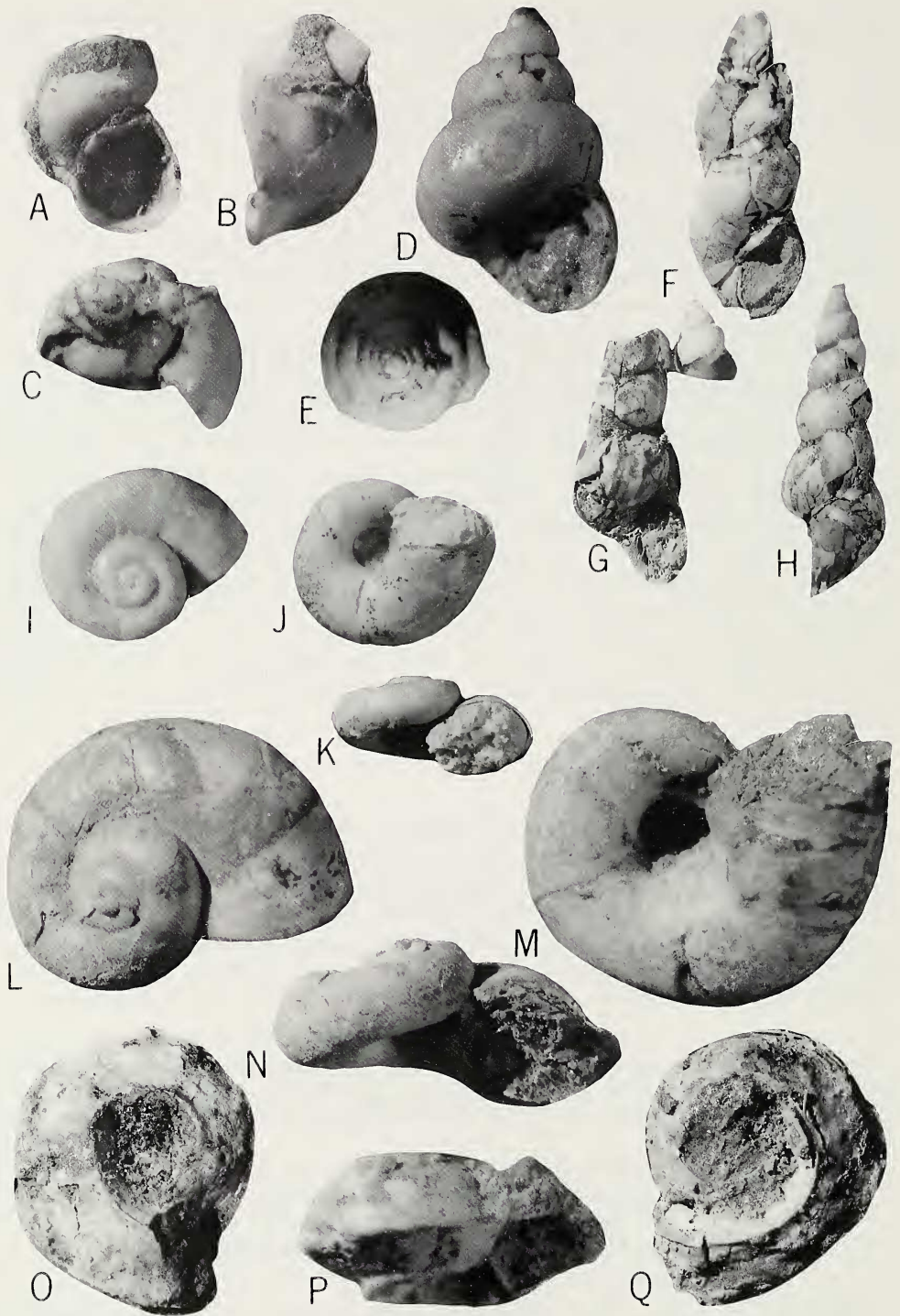


Fig. 14.—MESOGASTROPODA: HYDROBIIDAE. A–C: *Fluminicola? calderensis* n. sp. X10; A–B: Holotype (CM41684), A. apertural; B. lateral; C. Paratype CM 41685, apical; D–E: *Cincinnatia?* F–H: *Cincinnatia?* I: *Cincinnatia?* J: *Cincinnatia?* K: *Cincinnatia?* L: *Cincinnatia?* M: *Cincinnatia?* N: *Cincinnatia?* O: *Cincinnatia?* P: *Cincinnatia?* Q: *Cincinnatia?*

Description.—Shell small, bluntly conical, with four or more rounded whorls, initially regularly expanding, body whorl expanding rapidly, suture well impressed; nucleus small (0.25 mm) on plane of second whorl or very slightly elevated, embryonic whorls about 1.5, smooth, subsequent whorls shiny with very faint collabral wrinkles, strongest on body whorl, umbilicus narrow, covered by peristome, aperture subrectangular, parietal insertion of lip at near right angle to body whorl, peristome free of body whorl, thickened by inner callus, columellar lip thickened, reflected over and around umbilicus, basal and outer lip simple, thickened within, edge slightly blunt. Measurements of holotype: height, E3.4 mm, spire missing; width, 3.3 mm; height aperture, 2.0; width aperture, 1.8 mm; whorls unknown. Measurements of paratype: height, E3.0 mm, crushed; width, 2.9 mm; height aperture, 1.65 mm; width aperture, 1.0 mm; whorls ~4.2.

Discussion.—There is uncertainty with regard to generic assignment of this species. *Fluminicola? calderense* has many characteristics in common with both the genus to which it is tentatively assigned and to *Somatogyrus* Gill, 1863. *Fluminicola* was selected based on apertural characteristics, and the exclusively western distribution of this genus. *Somatogyrus* is, essentially, an eastern taxon. Among modern species, *F?. calderense* resembles both *F. fusca* (Haldeman, 1847), and *S. amnicoloides* Walker, 1915, but can be differentiated from *F. fusca* by its taller, convexly conic spire, oval aperture, and only slightly reflected columellar margin, and from *S. amnicoloides* by its much taller, convexly conic spire. Among fossil species, *F?. calderense* resembles some specimens of Pliocene *F. kettlemanensis* Pilsbry, 1934*a,b* from which it can be distinguished by the lower spire and more subrectangular aperture of *F. kettlemanensis*. According to Pilsbry (1934*a*:549), "There is no conchological difference between *Lithoglyptus* and *Fluminicola*, the distinction being in the form of the verge."

Etymology.—*calderense*, with reference to Calder Creek, a west side tributary of the North Fork of the Flathead River, near the type locality.

Environment and Distribution.—Living species of genus *Fluminicola* are restricted to the United States west of the Continental Divide, ranging from the Canadian border south to northern California, Nevada and Wyoming. It is found in a variety of habitats ranging from spring pools to medium-sized rivers (Burch, 1989:102). The geologic range is unknown.

Material.—Three specimens. Holotype CM 41684, spire missing, and paratype CM 41685, spire crushed, aperture damaged, are from W-2 (NFF-5) locality, British Columbia; additional specimen, PHDB-102, spire fragment, from Wurtz Bend (NDD-19) locality, Flathead County, Montana, all from Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Superfamily Valvatoidea Gray, 1840

Family Valvatidae Gray, 1840

Genus *Valvata* Müller, 1774

Type species.—*Valvata cristata* Müller, 1774.

Valvata procera (Russell, 1952), **new combination**
(Fig. 14.I–14.K)

Gyraulus procerus Russell, 1952:131,132, fig. 10, pl. 19, figs. 3–13; Ross, 1959:70.

Valvata procerus (Russell, 1952), Constenius et. al., 1989:197.

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bowmanana n. sp. Holotype (CM 41682), X10; D. apertural; E. apical; F–H: *Tryonia russelli* n. sp. X5, F. Holotype (KUMIP 289748), X5, apertural; G–H: Paratype CM 41680 with a spire fragment from lot Paratype CM 41681; G. apertural; H. combined for reconstructed lateral view. VALVATIDAE. I–K: *Valvata procera* (Russell, 1952) Hypotype (CM 41686), X10; I. apical; J. umbilical; K. apertural; L–N: *Valvata procera spatiosa* n. ssp. Holotype (CM 41688), X10; L. apical; M. umbilical; N. apertural. BASAMMATOPHORA: PLANORBIDAE. O–Q: *Helisoma triangulata* n. sp. Holotype (CM 41690), X10; O. left; P. apertural; Q. right.

Description-emended.—Shell small, depressed, of about three regularly expanding whorls, initial 1.2 whorls smooth, gradually acquiring costellae until, after about 1.75 whorls, sculpted with crowded fine, irregular and weak collabral costellae, most prominent on periphery; apex near planispiral for first 1.5 to 2.0 whorls, then subsequent whorls descend at increasing rate; whorls near circular, becoming slightly and obliquely oval at aperture, peristome complete, narrowly appressed to penultimate whorl, umbilicus open, about 1/5 diameter. Measurements of hypotype are as follows: diameter, major, 3.0 mm; minor, 2.3 mm; height 1.7 mm, H/D 0.57; whorls, 3.1.

Discussion.—This little valvatid is widely dispersed in the Kishenehn Basin, found at nearly all localities with suitable environments. Among living or more recently fossil valvatids, *V. procera* resembles *V. humeralis* Say, 1829, differing in being smaller, having fewer whorls, a more depressed shape, and more noticeably oval aperture. *Valvata humeralis* is one of the western group of valvatids. Among fossil valvatids, *V. procera* appears to be closest to Oligocene *V. paula* Pierce, 1993, from which it differs in being more depressed, less sharply sculptured, having a less rapidly descending ultimate whorl, and an oblique, bluntly oval aperture. Russell (1952:132; 1955:104–105) reported this species from his W-1 (type locality), and W-3 (later changed to C-3) localities, and from an outcrop near the mouth of Whale Creek, west bank of the Flathead River in Flathead County, Montana. These localities have been destroyed by erosion. The figured hypotype (CM 41686), although slightly crushed and from a different locality, appears representative of his type specimens.

Environment and Distribution.—*Valvata humeralis*, which may be the closest modern analog, is a western species, found from British Columbia and Montana south to California and New Mexico and into central Mexico (Bequaert and Miller, 1973:213), and is fossil, from the same general area, from Pliocene to Recent (Taylor, 1966). *Valvata*, in general, are inhabitants of well-vegetated lakes or slow flowing rivers, with little apparent preference in bottom conditions (Clarke, 1973). The genus *Valvata* is ancient, known from Jurassic to Recent, with several species from the Eocene-Oligocene.

Material.—More than 100 specimens. Figured specimen: Hypotype CM 41686 is from Bowman Creek (BWN-2) locality, Flathead County, Montana. Additional specimens, Hypotypes CM-41687 (18), KUMIP 289,751 (2), KUMIP 289,752 (18), PVLV-105 (4) from Bowman Creek locality; PVLV-106 from Wurtz Bend (NFF-19) locality; PVLV-107 from Kintla Creek Carnegie (KTL-1) locality; PVLV-108 (10) from Starvation Bend (NFF-12) locality, all Flathead County, Montana; and PVLV-109 (10) from Moose City North (NFF-9) locality; PVLV-110 (20) from Island (NFF-4) locality; PVLV-111 from E-4 (NFF-2) locality; PVLV-112 (20) from E-5 (NFF-1) locality; and PVLV-113 (20) from Commerce Creek (CMC-1) locality, all British Columbia. All specimens from Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Valvata procera spatiosa Pierce, **new subspecies**
(Fig. 14.L–14.N)

Diagnosis.—A *Valvata procera* in which the rate of expansion of the whorls increases more rapidly, with a marked increase after ~2.5 whorls.

Description.—Shell moderately sized, depressed, of about 3.5 whorls, first 2.5 whorls like the nominative form, at which point the rate of expansion of the subsequent whorl increases markedly, aperture round to slightly oval, peristome entire, scarcely attached to penultimate whorl, or barely detached. Measurements of holotype: diameter, major, 5.0 mm; minor, 3.6 mm; height, 3.0 mm; H/D 0.60; whorls, 3.5.

Discussion.—This valvatid is so unique, in size and shape (rate of expansion of whorls), when compared to the nominative species found at all other localities in the Kishenehn Basin that the first reaction is to consider it a different species.

However, detailed comparison under higher magnification showed that the initial ± 2.5 whorls are, although proportionately slightly larger, essentially identical. The marked distinction is in the even greater rate of expansion in the ultimate whorl. Considering the great polymorphism of some living valvatids, it is felt better to treat this taxon as a subspecies; however, whether it is, in fact, a true subspecies, or an ecophenotype, is impossible to ascertain. Although this taxon is found in close geographic proximity to the nominative form, limited faunal evidence suggests that the type locality may be of a slightly different age than adjacent localities. *Valvata procera spatiosa* bears a marked resemblance to fossil *V. humeralis densistriata* Pilsbry, 1934a;b from the Pliocene Kettleman Hills of California, differing in being somewhat larger, more depressed (H/W=0.60 versus H/W=0.90), and in lacking the sculpture of fine threads.

Etymology.—Latin, *spatiosa*, spacious, broad, large.

Environment and Distribution.—See above under *Valvata procera*.

Material.—Fourteen specimens. Holotype, CM 41688, and paratypes CM 41689, KUMIP 289,753, and PVLV 114, from W-2 (NFF-5) locality, British Columbia. Type horizon: Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Order Basommatophora

Superfamily Ancyloidea Rafinesque, 1815

Family Planorbidae H. and A. Adams, 1855

Note.—Taxonomy of the Planorbidae herein generally follows that of Hubendick, 1978.

Subfamily Planorbinae Pilsbry, 1934

Tribe Helisomatini Clarke, 1978

Genus *Helisoma* Swainson, 1840

Type species.—*Planorbis bicarinatus* Say, 1817.

Subgenus *Helisoma* (*s. str.*)

Helisoma triangulata Pierce, **new species**

(Fig. 14.O–14.Q)

Diagnosis.—A small, biconcave planorbid shell with three carina, one peripheral, one ringing a steep, deep umbilicus, the other ringing a deeply depressed spire.

Description.—Shell small, biconcave planorbid, of about four regularly increasing whorls, last 0.25 whorl increasing more rapidly; right side deeply and eccentrically depressed, sharply carinate on all whorls after embryonic whorls, sculpted with fine, closely spaced, prosocline costellae on last 1.5 whorls; left side deeply and steeply spirally umbilicate, sharply carinate at umbilical margin, sculpted with weak, straight radial costellae, third carina at periphery of whorls; aperture irregularly pentagonal, produced on right side, outer lip segments, between three keels, near straight on left side, broadly arched on right side. Measurements of holotype CM 41690: width 3.5 mm; height 2.3 mm; whorls est. 4. Range of paratypes: height 3.8–5.0 mm; width 2.3–2.6 mm, mostly crushed; whorls about 4.

Discussion.—The size and shape of this little species is so unique that it is not likely to be confused with any living species. It is a midget among the *Helisoma* and was initially considered to be a new genus of the Planorbidae, but further study of the specimens available showed that, despite its small size, it is really a *Helisoma* of the subgenus *Helisoma* (*s. str.*), and, in many ways, resembles some of the varieties of *H. anceps* Menke, 1830, which are known from strata as old as late middle Pliocene in Oregon (Taylor, 1966:35). It is, however, instantly differentiated by its small size, triple carina, deep spire depression and irregularly

pentagonal aperture. Fossil *Helisoma* are not common, and are not well understood, due in part to confusing taxonomy, and, in part, to the lumping of most planorbid genera into the inappropriate genus *Planorbis* Müller, 1774. In size, *H. triangulata* compares with Pliocene *H.*(?) *kettlemanense* Pilsbry, 1934a,b, but is instantly differentiated by the triple carina. *Helisoma triangulata* also bears a resemblance to modern *Helisoma* (*Carinifex*) *newberryi* (Lea, 1858), but can be easily differentiated by its size, medial keel and sunken apex.

Etymology.—Latin, *tri*, combining form of three and *angulata*, feminine, angular, referring to the distinctive triple keels or carinae of this species.

Environment and Distribution.—*Helisoma anceps* (*s. lat.*), which most closely resembles *H. triangulata*, is found in almost all permanent water situations with bottoms of all types and vegetation in various amounts. Distribution is from central and southern Canada, essentially throughout the United States, and into northwestern Mexico (Clarke, 1973:430–432). Modern shells were collected on the Flathead River in the Kishenehn Basin. The geologic range of the genus *Helisoma* is difficult to establish, since the proper taxonomic position of the many early Cenozoic “Planorbis” is uncertain, but surely extends back to early Pliocene *H.* (?) *kettlemanense*. The modern analog of this species, *H. anceps*, is known from the late middle Pliocene to Recent on the High Plains (Pierce, 1975:126).

Material.—Twenty-two specimens. Holotype, CM 41690 and all paratypes CM-41691 (6), KUMIP 289,754, KUMIP 289,755 (6), PPLN 113 (6), and PPLN-114 (2), are from W-2 (NFF-5) locality, British Columbia, Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Genus *Planorbella* Haldeman, 1842

Subgenus *Piersoma* Dall, 1905

Type species.—*Planorbis trivolvis* Say, 1816.

Planorbella fordensis Pierce, **new species**

(Fig. 15.D–15.G)

Diagnosis.—A moderate-sized, shallowly biconcave, thick-walled planorbid, whorls rounded, without carina, sculpted by weak spiral threads and moderate costellae.

Description.—Shell biconcave planorbid, of medium size, with about 4.25 expanding but modestly inflated thick-walled whorls of moderate axial height; right (umbilical) side shallowly and conically concave, hiding first whorl, whorls rounded, suture well impressed, sculpted with moderately strong prosocline costellae and weak spiral threads extending from suture to periphery, threads about six per mm on body whorl; left (spire) side very shallowly concave, whorls moderately rounded, suture impressed shallowly, all whorls visible, nuclear whorls about 1.5, smooth to finely punctate, subsequent whorls initially with fine, faint spiral threads, weak, shallowly prosocline costellae begin after second whorl, and are crossed by rare, discontinuous spiral threads, on body whorl, costae are irregularly interspersed among the costellae; aperture broken, but probably only slightly expanding. Measurements of holotype, an incomplete specimen: height >3 mm; width E10 mm; whorls >4.

Discussion.—Unfortunately, only two incomplete specimens of this most interesting species were found; however, they are sufficient to recognize a new species. *Planorbella fordensis* most resembles modern *P. subcrenulatum* (Carpenter, 1856), a western species, in shell shape, sculpture, and, from fragmentary evidence, aperture, but it can be distinguished by a much shallower concavity on the left side, and the sculpture of both prosocline costellae and spiral threads. The oldest probable *Piersoma* fossil appears to be early Pliocene *P. valens* Leonard and Franzen, 1944, from the Laverne Formation of Oklahoma. Except for size,

P. valens appears to be but weakly differentiated from *P. trivolvis*, found elsewhere in the latest Pliocene (Blancan) faunas east of the Continental Divide. *Planorbella fordensis* is grossly similar, but can be easily differentiated from *P. trivolvis* by its smaller size, and much finer sculpture and from both *P. trivolvis* and *P. valens* by the spiral threads.

Etymology.—*fordensis*, with reference to the type location near the mouth of Ford Creek, a tributary from the east of the North Fork of the Flathead River.

Environment and Distribution.—*Planorbella subcrenatum* is extremely tolerant, being found in swamps, ponds, streams, and rivers; mud substrates and abundant vegetation are preferred. Distribution western, from Yukon Territory to California and east to Manitoba and Minnesota (Clarke, 1973:458). As with the genus *Helisoma*, it is difficult to establish the geologic range of the genus *Planorbella*, since the proper taxonomic position of the many early Cenozoic “*Planorbis*” is uncertain, but it surely extends back to early Pliocene. *Planorbella subcrenatum* is known as fossil (as *P. subcrenata*) from two late Pliocene (Blancan) localities (Taylor, 1966:29, 70).

Material.—Two specimens. Holotype: CM 41694. Type locality: South Ford Creek (NFF-22) locality, Flathead County, Montana; Paratype CM 41695, an immature and/or broken back specimen of 2.25 whorls from E-3 (NFF-3) locality, British Columbia, both from Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Genus *Planorbula* Haldeman, 1840

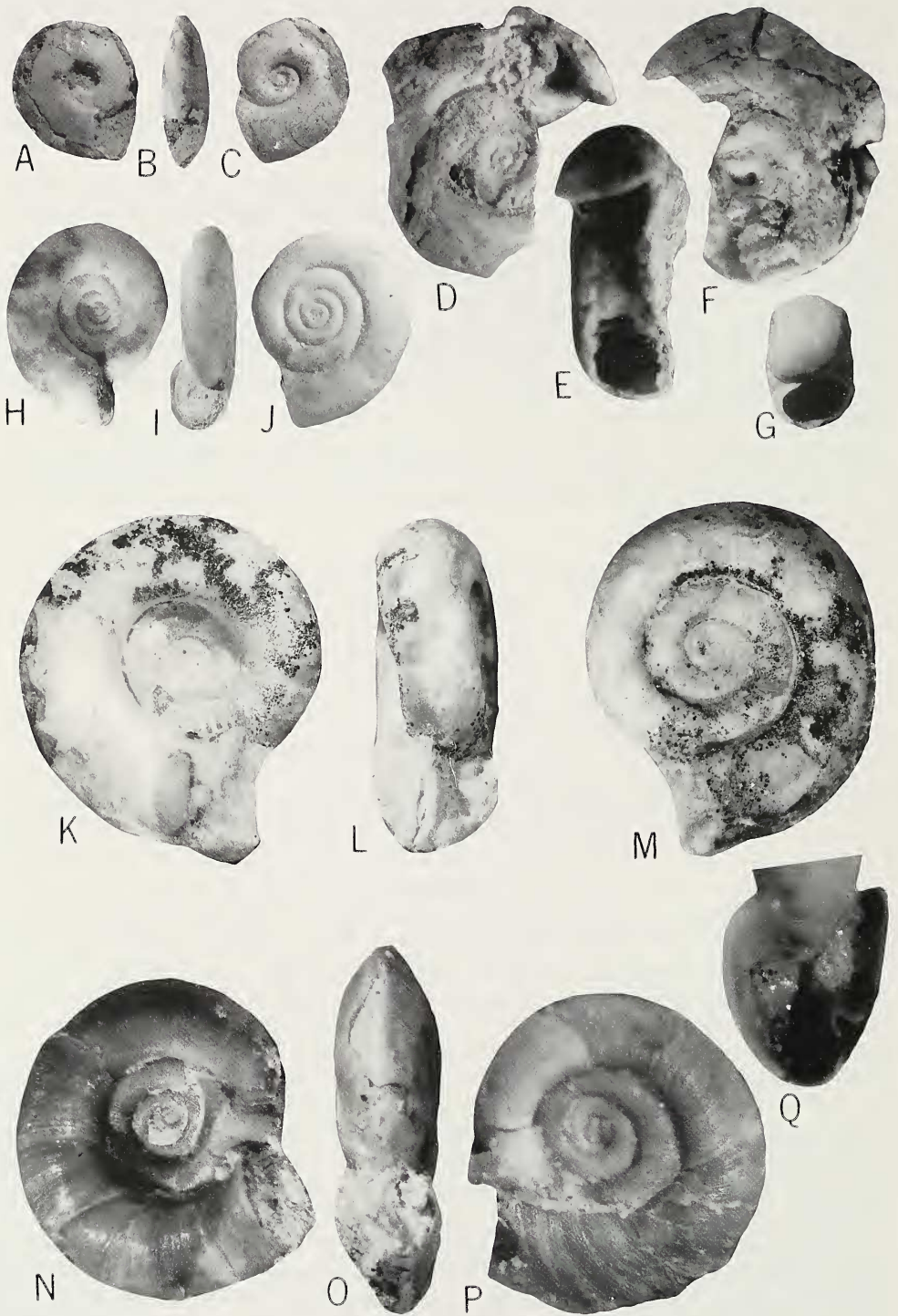
Type species.—*Planorbis armigerus* Say, 1821.

Planorbula, cf. *P. campestris* (Dawson, 1875)

(Fig. 15.K–15.M)

Discussion.—This is one of two fresh-water taxa considered, although reluctantly, to be inseparable from a living taxon. However, as previously noted, there is no implication that they are specifically identical biologically, merely indistinguishable conchologically, since there is no significant difference in shell morphology between these specimens and living specimens. The oldest *P. campestris* I have seen is from an early middle Pleistocene locality in North Texas (Pierce, 1975:41–44). Taylor (1966:83, 89) reported this taxon (also as cf.) from the middle(?) Pliocene near Jackson Hole, Wyoming. The only differences observable between the Kishenehn specimens and excellently preserved early Kansan specimens from the North Texas locality (above) were a slight tendency to some angularity at the periphery, and only vague spiral striae. The figured specimen, CM 41696, although partly a steinkern, cannot be separated from modern specimens. *Planorbula campestris* can be easily separated from *Biomphalaria haydeni* Pierce, 1993, with which it coexisted locally, by the almost flat right side, the slowly and regularly enlarging whorls, and the conically concave left side. *Planorbula campestris* resembles Oligocene *P. powelli* Pierce, 1993, from the Cabbage Patch fauna of southwest Montana, but *P. powelli* has a slightly concave right side and an angular aperture that is deflected to the left. Measurements of figured hypotype, CM 41696: width 4.2 mm; height 1.6 mm; W/H 2.62; whorls 3.75. Range of specimens: width 3.6–6.2 mm; height 1.3–1.7 mm; whorls 3.6–4.2.

Environment and Distribution.—Clarke (1973:424) found *P. campestris* in generally permanent waters such as swamps, flooded areas adjacent to ponds, roadside ditches, small ponds, and a slow-flowing small stream, all with mud bottom and abundant vegetation. It is a western species, found from British Columbia to



Manitoba and south to Utah and New Mexico (Clarke, op. cit.). The geologic range of the genus *Planorbula* is uncertain, due to taxonomic uncertainty resulting from the use of "*Planorbis*" for early Tertiary fossils, but it is known with certainty from the late Oligocene (*P. powelli*) of southwestern Montana, and from the middle Pleistocene of Texas (Pierce, 1975:128), and as *P. cf. P. campestris* from the middle to late Pliocene (Blancan) of Wyoming (Taylor, 1966:89).

Material.—Eleven specimens. Figured specimen, CM 41696, from Bowman Creek (BWN-2) locality, Flathead County, Montana. Additional specimens CM 41697 (2), and KUMIP 289,757 (2), from Bowman Creek (BWN-2) locality, KUMIP 289,758 (2) from Wurtz Bend (NFF-19) locality, and PPLN-115 (3) from Starvation Bend (NFF-12) locality (2), all Flathead County, Montana. PPLN-116, one specimen in matrix is from Commerce Creek (CMC-1) locality, British Columbia. All locations are in the Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Genus *Menetus* H. and A. Adams, 1855

Type species.—*Planorbis opercularis* Gould, 1847.

Subgenus *Menetus s. str.*

Menetus textus Pierce, **new species**

(Fig. 15.H–15.J)

Diagnosis.—A small planorbid with a flat right (umbilical) side and a shallow, widely concave left (spire) side, sculpted with fine, close costellae and more widely spread, cross-cutting, spiral lines, aperture deeply lunate-roundly ovate.

Description.—Shell small, planorbid, of about 4.5 rounded whorls, initial 1.5 to 1.75 whorls smooth; right side flat, whorls flatly rounded, suture moderately impressed, sculpture after embryonic whorls of fine, closely spaced, prosocline costellae cut by fine, more widely spaced, spiral lines, costellae becoming coarser and more widely spread in last 0.25 whorl; left side widely and shallowly concave, all whorls visible, whorls well rounded, embracing preceding whorl about 50%, sculpted with radial to orthocyrct costellae cut by fine, more widely spaced, spiral lines, costellae becoming coarser in last 0.25 whorl, interaction of costellae and lines give shell a fabric-like texture; aperture slightly expanded peripherally, deeply lunate-roundly ovate, advanced on right side, weak inner callus. Measurements of holotype, CM 41698: width, major 5.9 mm; width, minor 4.9 mm; height 1.6 mm; W/H 3.69; whorls 4.5. Range of paratypes: width 3.8–7.0 mm; height 0.7–est. 1.7 (crushed); W/H 3.68–4.22; greatest whorls 4.6.

Discussion.—Among modern species, *M. textus* appears related to the *M. cooperi* (Baker, 1945) group (*M. opercularis* of Burch, 1989:202), especially those subspecies with rounded peripheries, from which it can be differentiated in having more, and more slowly expanding, whorls, in lacking the spiral ridges below the slight shoulder, and in lacking the tendency to malleation on the base. Considering the size, prominent spiral lines, and the textile-like texture of the shell of *M. textus*, the only fossil species with which it could be confused is lower Eocene "*Planorbis*" *storchi* Russell, 1931 (most probably a *Biomphalaria*), which is twice as large, 13mm in width and 3.3 mm in height.

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Fig. 15.—BASAMMATOPHORA: PLANORBIDAE. A–C: *Menetus hilli* n. sp. Holotype (CM 41692), X5; A. left; B. apertural; C. right; D–G: *Planorbella fordensis* n. sp. D–F: Holotype (CM 41694), X5; D. left; E. apertural; F. right; G. *P. fordensis* paratype (CM 41695), X10, apertural view of juvenile; H–J: *Menetus textus* n. sp. Holotype (CM 41698), X5; H. left; I. apertural; J. right; K–M: *Planorbula* sp. c.f., *P. campestris* (Dawson, 1875) Hypotype (CM 41696), X11; K. left; L. apertural; M. right; N–Q: *Biomphalaria haydeni* Pierce, 1993; N–P: Hypotype (CM 41700), X10; N. left; O. apertural; P. right; Q. *B. haydeni* Hypotype (PPLN-108), X15, aperture showing basal and two palatal lamella, lower hollow.

Environment and Distribution.—The suggested modern analog, *Menetus cooperi*, is relatively common in California, Oregon, and Washington, and ranges north to Alaska and east to Alberta (Clarke, 1973:418). Clarke (op. cit.) collected specimens from a small stream and a moderate-sized lake, both with sand bottom and sparse vegetation. Previously known geologic range of the genus is from early Pliocene to Recent.

Etymology.—Latin, *textus*, p.p. of *texto*, fabric, woven cloth, with reference to the surface texture of the shell.

Material.—Eight specimens. Holotype, CM 41698 and paratypes CM 41699, KUMIP 289,759 (2), and PPLN-117 (1+3 fragments) are all from Wurtz Bend (NFF-19) locality, Flathead County, Montana, Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Subgenus *Micromenetus* F. C. Baker, 1945

Type species.—*Planorbis dilatatus* Gould, 1841.

Menetus hilli Pierce, **new species**

(Fig. 15.A–15.C)

Diagnosis.—A small, lenticular, ultradextral species with spire in a spirally enlarging, near vertically walled pit, with near 90° shoulder as whorl expands to a roundly angular periphery, aperture roundly triangular, advanced on basal side.

Description.—Shell small, lenticular, modestly hyperstrophic (ultradextral), of four or more rapidly expanding whorls; spire (left side) deeply depressed, in a spirally enlarging, near vertically walled pit, whorls strongly shouldered at about 90° departing pit, thence shallowly convex to a medial, roundly angular, periphery; embryonic whorls granulose, subsequent whorls with weak collabral wrinkles, becoming closely and weakly ribbed dorsally; base (right side) shallowly concave, whorls moderately overlapping, smoothly convex and faintly wrinkled between periphery and moderately impressed suture; aperture roundly triangular, moderately overlapping penultimate whorl on both sides, advanced on basal side. Measurements of holotype: height 1.8 mm; width, major 4.5 mm; minor 3.5 mm; whorls 3.75.

Discussion.—*Menetus hilli* differs from *Menetus textus* in size, in that its left side (spire) is narrowly and relatively deeply sunken while its right side (umbilicus) broadly and shallowly concave and in having a roundly angular, medial carina on the ultimate whorl. Among living species of *Micromenetus*, it is closest to *M. brogniatianus* (Lea, 1842), which differs in having a near flat to only slightly concave right side, and an aperture produced markedly to the left side. Its roundly, but symmetrically, triangular aperture, appears unique among the members of this genus. *Menetus hilli* is also quite similar to *Promenetus exacuus* (Say, 1821), but lacks the flat spire, slightly descending aperture, more carinate periphery, and, commonly, a malleated appearance to the left side of *P. exacuus*. The exact relationship between the genera *Menetus* (s.l.) and *Promenetus* is unclear and deserves study.

Etymology.—Named to honor Warren Hill, fellow geologist, close friend and retired National Park Service Superintendent.

Environment and Distribution.—*Menetus* (s. lat.) is not well known. *Menetus* (s. str.) is a western taxon, distributed from Alaska to California, but not often east of the Rocky Mountains. *Micromenetus* is eastern in distribution, from Maine to Florida, generally east of the Mississippi River, except for Iowa to Texas (F. C. Baker, 1945:182–190; J. B. Burch, 1989:202). The ecology of *Menetus* is not well known. Clarke (1973:418) suggests it to be a denizen of shallow streams and ponds, with sand bottoms, and sparse vegetation. Geologic range is unclear,

probably due to confusion with *Promenetus exacuus*. F. C. Baker (1945:187; 190) states "Pliocene to Recent."

Material.—Four specimens. Holotype, CM 41692, and paratypes, CM-41693 and KUMIP 289756 (2) from W-2 (NFF-5) locality, British Columbia, in Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Tribe Biomphalarini Hubendick, 1955

Genus *Biomphalaria* Preston, 1910

Type species.—*Biomphalaria smithi* Preston, 1910.

Subgenus *Tropicorbis* Brown and Pilsbry, 1914

Type species.—*Planorbis liebmani* Dunker, 1850 (= *P. havanensis* Pfeiffer, 1839).

Environment and Distribution.—Subtropical and tropical, generally in mud-bottomed freshwater marshes and bayous; they are well adapted to desiccation and capable of tolerating near freezing temperature briefly; distributed from South America, Caribbean, Central American and Gulf Coast of North America as far north as Baton Rouge, LA and Austin, TX (C. S. Richards, 1963). *Tropicorbis* is known from Oligocene [*B. nebraskensis* (Evans and Schumard, 1854) and *B. havdeni* Pierce, 1993] and, questionably in this subgenus, ?Eocene *B. storchi*, (Russell, 1931), (Pierce, 1993:984, 987).

Biomphalaria haydeni Pierce, 1993

(Fig. 15.N–15.Q)

Discussion.—These specimens are but slightly differentiated from those at the type locality in the late Oligocene (Arikarean) Cabbage Patch beds of southwestern Montana (Pierce, 1993:983, 984), but the differences are so slight as to not suggest any separate taxonomic status. These slight differences include a wider range of angularity at the periphery, from almost round to quite sharp, a greater W/H in those with angular forms, a flatter right side, slightly more prominent costellae and an even greater frequency of irregular growth than observed within the type lots. These growth irregularities are usually due to abrupt changes in rate of coiling, leading to marked differences in overlap by succeeding whorls. Only one specimen displayed part of the apertural denticles, and, in it, the palatal (right side) lamellae are both slightly stronger than those observed in the type specimens. Extreme specimens with the most acute peripheries from the Kishenehn Basin, could, in gross appearance, be confused with some varieties of *Promenetus exacuus* (Say, 1821), but, even if the apertural lamellae are not apparent, could be easily separated from the flat to slightly domed whorls on the right side of *P. exacuus*. Measurements of the figured hypotype, CM 41700: width 4.6 mm; height est. (slightly crushed) 1.5 mm; W/H 3.07; whorls 4. Range of hypotypes: width 3.4–5.2 mm; height 1.1–est. 1.6; W/H 3.09–3.25; whorls 3.5–4.5.

Material.—More than 60 specimens. Figured specimen, CM 41700 and CM 41701 (14), PPLN 119 and PPLN 120 (2) from Bowman Creek (BWN-2) locality, Flathead County, Montana. Additional specimens are as follows: PPLN-120 (25) from South Ford Creek (NFF-22) locality; KUMIP 289,760 and KUMIP 289761 (14) from Wurtz Bend (NFF-19) locality; and PPLN-121 (8) from Starvation Bend (NFF-12) locality, all Flathead County, Montana; and PPLN-122 from Moose City North (NFF-9) locality, British Columbia. All localities are in Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Biomphalaria spira Pierce, new species
(Fig. 16.A–16.C)

Diagnosis.—A depressed biomphalarid with flat oval whorls and aperture, whorls scarcely overlapping, aperture not deflected from axis of shell.

Description.—Shell a medium-sized, depressed planorbid, of about five or more slowly expanding oval whorls; right side slightly sunken, all whorls visible, whorls flatly rounded, scarcely embracing previous whorl, suture impressed, sculpture of weak, fine, regular, prosocline costellae; left side very shallowly and widely concave, all whorls visible, whorls flatly oval, suture moderately impressed, sculpture of weak, fine, regular, near radial costellae; aperture elongate and flatly oval, advanced on right side, not deflected from axis of shell, last 0.5 mm slightly thickened and sculpted with more widely spaced costellae, bearing one or more teeth, a blunt, spirally elongated tooth is located about 0.5 mm behind aperture on left side. Measurements of holotype, CM 41702: width 9.0 mm; height crushed; whorls ~5.3. Apertural measurements of paratype: width 2.8 mm; height 1.5 mm.

Discussion.—All specimens at hand are crushed, except for the aperture and a portion of the ultimate whorl of paratype CM 41702, from which the distinctive flatly oval shape of the whorls at, and just behind the aperture is apparent. This specimen also shows an apertural denticle, and what may be the root of a broken-off, thin spiral denticle, about 0.5 mm long, on the right side of the penultimate whorl. This species generally resembles *B. kishenehnsis* (Russell, 1952), which Russell (1952:130,131) found at his W-1 and C-3 localities in British Columbia, and is very common at many localities of the Middle Fork Kishenehn Basin. *Biomphalaria kishenehnsis* is a much larger species, exceeding 35 mm with >6 whorls, bearing stronger costellae, and a heart-shaped cross section due to a mild peripheral angularity and only slight embracement of the preceding whorl. "*Planorbis*" *cirrus* White, 1877b, also bears a strong resemblance, but has more whorls, somewhat slower expansion of whorls, and a more rounded whorl section. Among modern species, *B. spira* closely resembles some forms of *B. orbiculus* (Morelet, 1849) in the flat oval cross section of the whorls, but is generally smaller, more depressed, and succeeding whorls of *B. spira* embrace preceding whorls to a greater degree.

Environment and Distribution.—Richards (1937:255) found shells of *B. orbiculus* abundant in dried swamps on the Island of Cozumel, Quintana Roo, Mexico. It is generally distributed along the Gulf Coastal region of Mexico, and on the Yucatan Peninsula (Baker, 1945). "*Planorbis*" *cirrus* is known only from the middle Eocene (?Uintan-Bridgerian) of southwestern Wyoming (Henderson, 1935:245).

Etymology.—Latin, *spira*, fem., coil, as of a serpent, or a rope, with reference to the flat, coiled appearance of this species.

Material.—Five specimens. Holotype, CM 41702, is from South Ford Creek (NFF-22) locality; paratypes, CM 41703, KUMIP 289,762, KUMIP 289,763, and PPLN-123 are from Starvation Bend (NFF-12) locality (4), Flathead County, Montana, Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Subgenus *Australorbis* Pilsbry, 1934c

Type species.—*Planorbis guadalupensis* Sowerby, 1822 (= *P. glabratus* Say, 1818).

Environment and Distribution.—A tropical lake and river dweller, also found in marshes and bayous of South America and the Antilles. *Biomphalaria glabrata* (Say, 1818), a common modern species, is an extremely temperature sensitive species. Reproduction is limited to a water temperature range of between 20°C

and 30°C, and death occurs rapidly at temperatures of 5°C (Taylor, 1985:269). Fossil *Australorbis* are relatively common among Eocene faunas of the west, e.g., *B. spectabilis* (Meek, 1860*b*), *B. utahensis* (Meek, 1860*b*), and *B. convolutus* (Meek and Hayden, 1856).

Biomphalaria kishenehnensis (Russell, 1952)
(Fig. 16.D, 16.E)

Planorbis kishenehnensis Russell, 1952:130–131; 1956:104–108.

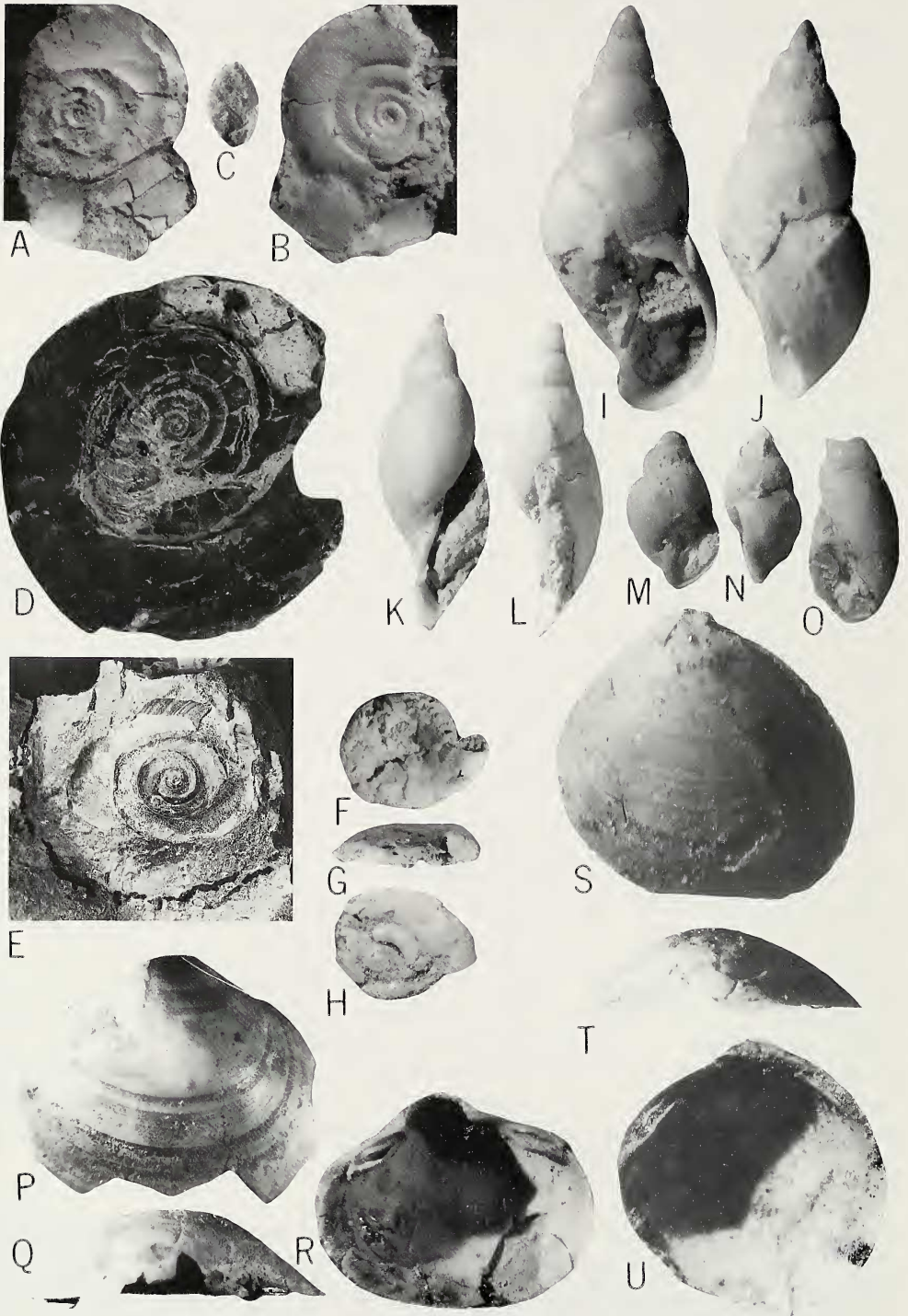
Australorbis pseudoammonius (Schlotheim, 1820). Taylor, *in* Ross, C. P., 1959:70–71; Taylor, 1975:211.

Biomphalaria kishenehnensis (Russell, 1952). Pierce, *in* Constenius et. al., 1989:197–198; Pierce, 1993:984.

Discussion.—Russell (1952:130–131; 1956:104–106) reported this species from his localities W-1, E-3, C-1, C-3 (originally W-3 locality, his type locality), and an unnamed locality on the North Fork of the Flathead River in Montana just upstream of the mouth of Whale Creek (USGS 20198, Taylor, 1975:213). Spring floods and mass movements in the years since Russell made his collections have vastly altered the cut banks along the river. Of the localities listed above, W-1, C-1, and C-3 are destroyed or buried and the remnants of E-3 now contain a mostly terrestrial fauna. Only at Hook locality, across the river and slightly upstream from Russell's Whale Creek locality, but in a lithologically similar unit, have examples of *B. kishenehnensis* been found in the North Fork Basin. However, this species is commonly encountered at several, as yet undescribed, localities on the Middle Fork Basin (Fig. 16.D, from Coal Creek locality on Middle Fork). The material at hand, though limited, is adequate to confirm Russell's Description and Remarks (1952:130–131; 1956:107–108), and his conclusion that *B. kishenehnensis* is closely related to, but distinct from, middle Eocene (Bridgerian) *B. spectabilis* (Meek, 1860*b*).

Taylor (*in* McKenna et al., 1962) attempted a very broad revision of the fossil taxa within this genus. Basically, he decided that every large planorbid, "with numerous closely coiled whorls, nearly plane right side, concave left side, with a subangulation or abrupt curve next to the suture, and smooth nuclear whorls lacking carination" (*Ibid.*, p. 8) constituted a single species, and that species was identical to the European "*Planorbina*" (*Biomphalaria pseudoammonius* (Schlotheim, 1820). A diagnosis this broad is more suitable at subgenus or genus level than to define a species. Such diverse and readily separable taxa as *Biomphalaria convolutus* (Meek and Hayden, 1856), *B. spectabilis* (Meek, 1860*b*), *B. utahensis* (Meek, 1860*b*) and *B. kishenehnensis* (Russell, 1952) would become subspecies, or, perhaps, simply local forms of a global species. I find this approach unacceptable, and reject this synonymization.

Material.—Two specimens, CM 41704 and KUMIP 289,764, both fragmentary and incomplete, from Hook (NFF-26) locality, Flathead County, Montana, Lower Member, Kishenehn Formation, late Eocene. Figured specimen PPLN-125, of *B. kishenehnensis*, is from the Coal Creel locality in the Middle Fork part of Kishenehn Basin, some 22 km southeast of the Hook locality, where it is abundant, and is provided for comparison.



Tribe Planorbini Clarke, 1973
Genus *Gyraulus* Agassiz in Charpentier, 1837

Type species.—*Planorbis albus* Müller, 1774.
Subgenus *Torquis* Dall, 1905

Type species.—*Planorbis parvus* Say, 1817.

Environment and Distribution.—Gyraulids of the subspecies *Torquis* prefer shallow, quiet, well-vegetated ponds with almost any bottom, although mud seems to be preferred (Baker, 1928:377). Distribution is general in North America from Alaska to Sonora, Mexico, and Cuba (Bequaert and Miller, 1973:205). Previously known geologic range is uncertain, certainly since early Pliocene, possibly much older.

Gyraulus, cf. *G. scabiosus* (Hanna, 1922)
(Fig. 16.F–16.H)

Planorbis (Torquis) scabiosus Hanna, 1922:4, 5, pl. 1, figs. 4–6.

Discussion.—Hanna's description and illustration of this species from an undescribed bed of the Pliocene(?) Warner Lake beds of eastern Oregon matches almost exactly the specimens found in the Kishenehn Basin, especially in the shape of the aperture and the overlapping and abutting nature of the suture on the left side of these specimens. The description of the sculpture should be expanded to specify prosocline costellae on the right side that become radial to ophistocyrts after crossing the rounded perimeter of the whorls, and that the aperture is lunate-roundly ovate, advanced on the right side. There is no modern *Gyraulus* that has this exact combination of features. Measurements of figured hypotype, CM 41705: width 4.2 mm; height 1.2 mm; whorls ~3.5, nucleus damaged.

Material.—Nineteen specimens. Figured specimen, CM 41705, and KUMIP 289,765 are from Commerce Creek (CMC-1) locality, British Columbia. Additional specimens are as follows: CM 41706 from E-5 (NFF-1) locality (1+2 fragments); PPLN-126 (2) from E-4 (NFF-2) locality, both British Columbia; and PPLN-127 (4) from Kintla Creek Carnegie (KTL-1) locality; KUMIP 289,766 (3) and PPLN-128 (4) from Wurtz Bend (NFF-19) locality; and PPLN-129 (3) from Starvation Bend (NFF-12) locality, Flathead County, Montana, and all from Lower Member, Kishenehn Formation, late Eocene-Oligocene.

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Fig. 16.—BASAMMOTOPHORA: PLANORBIDAE. A–C: *Biomphalaria spira* n. sp. A–B: Holotype (CM 41702), X4; A. left; B. right; C. *B. spira* Paratype KUMIP 289763, X5, section through ultimate whorl behind aperture; D, E: *Biomphalaria kishenehnensis* (Russell, 1952); D. Hypotype PPLN-125, x2, left; E. Hypotype CM 41704, X1.5, interior of left side; F–H: *Gyraulus* sp., c.f. *G. scabiosus* (Hanna, 1922) Hypotype (CM 41705), X5; F. left; G. apertural; H. right. LYMNÆIDAE. I–J: *Lymnaea bowmanana* n. sp. Holotype (CM 41707), X5; I. apertural; J. lateral; K–L: *Lymnaea newmarchi* (Russell, 1952) Hypotype (CM 41709), X5; K. apertural; L. lateral; M–N: *Lymnaea lacerta* n. sp. Holotype (CM41711), X5; M. apertural; N. lateral. PHYSIDAE. O. *Aplexa* sp., c.f. *A. hypnorum* (Linnaeus, 1758) Hypotype (CM 41713), X5, apertural. BIVALVIA: SPHAERIIDAE. P–R: *Sphaerium progrediens* Russell, 1952; P–Q: Hypotype (CM 41715), X5; P. exterior of right valve; Q. umbonal of right valve; R. *S. progrediens* Hypotype (KUMIP 289774), X5, interior of left valve; S–U: *Sphaerium discus* n. sp., left valve Holotype (CM 41717), X10; S. exterior; T. umbonal; U. interior.

Family Physidae Fitzinger, 1833

Genus *Aplexa* Fleming, 1820*Type species.*—*Bulla hypnorum* Linné, 1758.*Aplexa* sp., cf. *A. hypnorum* (Linné, 1758)

(Fig. 16.O)

Discussion.—Although a rarely encountered species in the Kishenehn localities, and despite not having at hand a “perfect” specimen, I have no hesitation in referring these specimens conchologically to the genus *Aplexa*, and they compare favorably with modern *A. hypnorum*. I have compared these specimens with several lots of late Pliocene to modern *A. hypnorum* specimens from High Plains localities that are in my reference collection. Other than being slightly more slender, on an average, no significant difference can be discerned. This is yet another of the taxa in this Kishenehn fauna the appears to have survived unchanged conchologically from ?late Eocene to the Recent. As elsewhere stated, this does not imply biologic specific identity. Of the four specimens at hand, two are juveniles, heights 2.6 mm and 3.3 mm, with 2.5 to 2.75 whorls. The largest specimen, from Bowman Creek locality, has both apical and basal breakage, but is estimated at a height of 7 mm with 3.5 to 4 whorls. The previously known geologic range of this species is from late Pliocene, Blancan (Pierce, unpublished data) to modern. However, this is probably the same as *Aplexa* indet. reported by C. P. Ross (1959:70–71) from his Locality 14778, which is very near our Bowman Creek (BWN-2) locality. Among fossil sinistral taxa, two Cretaceous species, *Bulinus atavus* White, 1877a, now considered an *Aplexa*, and *B. disjuncta* White, 1877b, now considered a sinistral *Lymnaea* (Pierce, 1996), are most similar. Both are much larger than *A. hypnorum*. Although Clarke (1973:383) reports height up to $\frac{3}{4}$ inch for *A. hypnorum* in Canada, fossil and modern shells from the High Plains seldom exceed 7 mm in height, which is the estimated height of the largest specimen from Bowman Creek locality. In addition to size, *Aplexa atava* is a considerably more elongate species, with a W/H of only 0.33, compared with 0.40 to 0.45 for *A. hypnorum*. *Lymnaea disjuncta* can be distinguished by its inflated body whorl and prominent columellar plication. Russell (1956:104–108), reported a *Physa*? from his C-3 locality in British Columbia, and from an unnamed locality on the west bank of the Flathead River near the mouth of Whale Creek. His restoration is of a much larger physid, more similar to some of the slender morphs of *Physa gyrina* Say, 1821. A physid of this character was not encountered as part of this study.

Environment and Distribution.—This is a species of seasonal streams and pools, often with mud bottom, occasionally from small, clean brooks with mud bottom. Distribution is holarctic, in North America from the Arctic Ocean south to Colorado and Utah in the west and to about the Ohio River in the east, and from Washington east of the Cascades east to the Atlantic Ocean (Baker, 1928:474; Taylor, 1966:110). Geologic range of the genus is unclear, since the true taxonomic position of many late Mesozoic and early Cenozoic species variously assigned to the genera “*Bulinus*”, *Physa*, and *Aplexa* is unresolved. It may extend from Cretaceous to Recent; for *A. hypnorum* it is certainly from late Pliocene to Recent.

Material.—Four specimens. Figured specimen CM 41713 is from Bowman Creek (BWN-2) locality, Flathead County, Montana. Additional specimens are as follows: KUMIP 289,773 from E-4 (NFF-2) locality, British Columbia; and CM 41714 (2) from Starvation Bend (NFF-12) locality, Flathead

County, Montana. All specimens from the Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Superfamily Lymnaeoidea
Family Lymnaeidae Rafinesque, 1815
Genus *Lymnaea* Lamarck, 1799

Type species.—*Helix stagnalis* Linné, 1758.

Discussion.—The lymnaeids are notorious for having highly variable shell forms (ecophenotypes) within the confines of an single anatomical species. As a result, there is a plethora of “species” based on variations of shell form. Hubendick (1951), based on anatomical studies, recognized only the genera *Lanx* Clessin, 1882, and *Lymnaea* in North and Central America, with only 13 species (two questionable) within the latter, and illustrated the known range of shell variability for each species. The species recognized by Hubendick closely approximate the “groups” as used by Baker (1911, e.g., p. 298). For paleontological usage, since anatomical character for determination of species is not possible, defining “species” as members of “groups” based on the defined range of shell variability for a modern species (*sensu* Hubendick, 1951) appears to be the most workable solution (Pierce, 1993:984–985). This usage appears to have no effect on environmental or ecological considerations.

Group of *Lymnaea palustris* (Müller, 1774)

Discussion.—The shell of this group is one of the most clear-cut and easily defined of the lymnaeids (see Hubendick, 1951:119–120 for diagnosis.)

Environment and Distribution.—Prefers lakes of any size, well vegetated, clear, or stagnant. Malleated forms are typical of stagnant water and muddy bottoms (Baker, 1911:331). Distribution holarctic, in North America, south to California, New Mexico, and Missouri, thence northeast to Nova Scotia (Hubendick, 1951: fig. 304). The genus *Lymnaea* is ancient, extending back at least as far as Jurassic. Since there has been no comprehensive study of fossil lymnaeids, the range of the various Groups is not clear. The Group of *L. palustris* extends back to Eocene (Bridgerian), at least with *L. vetusta* Meek, 1860*b*.

Lymnaea bowmanana Pierce, **new species**
(Fig. 16.I, 16.J)

Diagnosis.—Shell elongate conic, of six or more moderately rounded whorls, spire high, acute, aperture elongate ovate-lunate, columellar and basal lips expanded.

Description.—Shell dextral, of moderate size, elongate conic, spire high, acute, $\leq 45^\circ$, whorls six or more, moderately rounded, slightly shouldered, rapidly elongating, suture moderately impressed, occasionally appearing flanged and/or crenulated, nucleus small, diameter ~ 0.25 mm, nuclear whorls about 1.5, smooth and shining, subsequent whorls with fine growth costellate, sharpest near suture, blurring to wrinkles below periphery of whorl, last whorl often malleated, narrowly umbilicate. Aperture elongate, $Ha/H \geq 0.40$, narrowly ovate-lunate, outer lip thin, sharp, simple, basal lip widely but shallowly reflected, columellar lip expanded, rolled over and obscuring umbilicus, columella with prominent plication just below parietal margin. Measurements of holotype: height, 11.3 mm; width 4.7 mm; height of aperture, 4.8 mm; W/H 0.40; Ha/H 0.41; whorls 6.1. Largest specimen observed is 18.5 mm in height from South Ford Creek locality.

Discussion.—This species is one of the most widely distributed lymnaeids in the Kishenehn basin. It resembles, of course, all other members of the group of

Lymnaea palustris. Among fossil members of this group, *L. bowmanana* most resembles Eocene *L. vetusta* Meek, 1860b, and Oligocene *L. ambiguospira* Pierce, 1996, both in the group of *L. palustris* (Pierce, 1993:985–986). *Lymnaea bowmanana* can be easily distinguished from them by its shorter, narrowly ovate-lunate aperture, and flared, spoon-shaped basal lip. Among modern “species” of the *L. palustris* Group, it most resembles *L. elrodiana* Baker, 1935, which has a more widely ovate-lunate aperture and less prominently flared basal lip. It is most interesting to note that *L. elrodiana* is living in nearby Lake McDonald (Elrod, 1902), part of the Flathead River drainage system.

Etymology.—*bowmanana*, with reference to the type locality on Bowman Creek, a tributary of the North Fork of the Flathead River, Montana.

Material.—More than 140 specimens. Holotype CM 41707 from Bowman Creek (BWN-2) locality, Flathead County, Montana, Lower Member, Kishenehn Formation, late Eocene-Oligocene. Paratypes: KUMIP 289,768 (8) and PLYM-116 (13), from Bowman Creek (BWN-2) locality; KUMIP 289767 and PLYM-117 (6) are from South Ford Creek (NFF-22) locality, CM 41708 (8) and PLYM-118 (50) are from Wurtz Bend (NFF-19) locality, all Flathead County, Montana; PLYM-119 from Moose City North (NFF-9) locality; PLYM-120 from W-2 (NFF-5) locality; PLYM-121 from E-2 (NFF-6) locality; and PLYM-122 (>50) from E-4 (NFF-2) locality, all British Columbia. All localities in Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Group of *Lymnaea catascopium* Say, 1817

Discussion.—This group is highly variable in shell form, but is generally distinguished by an “aperture ovate or long ovate, somewhat produced and effuse anteriorly, as long as, or longer than the spire; . . . inner lip narrow, reflected and appressed tightly to the columellar region, either completely closing the umbilicus or leaving a very small, narrow chink; columella with a heavy oblique plait causing the axis to be twisted; . . .” (Baker, 1911:382). In this group, the fusiform shape and elongated aperture are key traits.

Environment and Distribution.—Characteristic of larger lakes, rivers and bays, often near shore, on most bottoms, but seems to prefer a rocky shoreline (Baker, 1911:387). A North American group with main distribution in north central United States and south central Canada, with outlying species from British Columbia to California and east to Utah (Hubendick, 1951:fig. 315). Geologic range is uncertain.

Lymnaea newmarchi Russell, 1952

(Fig. 16.K, 16.L)

Emended description.—“Shell small, slender, narrowly elongate conic, spire high and acute, spire angle $<40^\circ$, with about five whorls, nucleus small, ~ 0.30 mm, nuclear whorls about 1.5, smooth to granular, subsequent whorls becoming flatly rounded, suture shallow, the body whorl rather elongate. Aperture narrowly ovoid, the length exceeding that of the spire, $Ha/H > 0.50$, narrowly and acutely angled at apex, parietal callus continuous, inner lip narrow but thickened, a solid, sinuous extension of columella, completely obscuring umbilicus, with a slight plication just in front of the parietal portion, basal lip weakly but broadly reflected, elongating aperture. Surface marked by fine, rather regular growth lines, strongest near suture, variable on remainder of whorl, ranging from continuing undiminished onto basal portion of whorl to becoming indistinct fine growth wrinkles, strongest on body whorl beginning below sutural flange; color white to pale bluish gray, but some specimens with pink coloring, which marks the growth lines and also appears as fine revolving lines” (after Russell, 1952: 103, emendations in italics). Measurement of hypotype: height 9.6 mm; width 3.3 mm; height aperture 5.6 mm; W/H 0.34; Ha/H 0.58; whorls 4.7, outer and basal lip of aperture missing. Largest specimen observed, 18.0 mm, crushed, is from Starvation Bend locality.

Discussion.—Russell’s (1952:129–130) original description was based on an

immature specimen of only four whorls, although he had a larger specimen ($h=11.0$ mm). Russell's type locality, apparently on a displaced slide block, has been eroded away. *Lymnaea newmarchi* appears to be of the *Lymnaea catascopium* group, although resembling several of the more slender morphs of the modern *L. palustris* group, such as *L. elodes* Say, 1821 and *L. exilis* Lea, 1834. Although the spires of both are very similar to *L. newmarchi*, their apertures are much shorter, and, comparatively, more inflated, and both fall short of the exaggerated reflected flare of the basal lip that so elongates the aperture of *L. newmarchi*. Most similar is *L. sumassi* Baird, 1863, from British Columbia and Utah, whose taxonomic position is open to some question, e.g., Hubendick (1951:205) considers it a *L. palustris*, whereas Baker (1911:XV, 403) lists it as a member of his Group of *Catascopium*. Considering Hubendick (1951:130) adopted Baker's (1911:382) description of *L. catascopium*, and the apertural characteristics tend to support Baker's choice, it is adopted herein. *Lymnaea sumassi*, especially the type specimens illustrated by Baker (1911:pl. 41, figs. 11–14) differ only in being much larger and having a somewhat shorter, more inflated aperture. Among the older fossil lymnaeids with characteristics similar to *L. newmarchi*, only Eocene *L. vetusta* and Oligocene *L. ambiguospira* are close enough for comparison. *Lymnaea newmarchi* can be easily differentiated by its more slender shape, flatly rounded whorls, and slender, elongate aperture. Pleistocene *L. nashotahensis* Baker, 1909, from Wisconsin, considered a *L. palustris* by Hubendick (1951:196), is remarkably similar, but has more rounded whorls, a shorter, inflated aperture and "... an umbilical chink which is usually absent in *catascopium*" (Baker, 1911:109). In short, the exaggerated character of the aperture of *L. newmarchi* appears unique among the lymnaeids.

Material.—More than 30 specimens. Figured specimen, CM 41709, and KUMIP 289,770 (2) are from Wurtz Bend (NFF-19) locality, Flathead County, Montana. Additional specimens: CM 41710 (3) and PLYM-123 (12 cr.) are from Starvation Bend (NFF-12) locality, Flathead County, Montana; KUMIP 289,769, PLYM-124 (11) are from E-5 (NFF-1) locality (11); and PLYM-125 from Commerce Creek (CMC-1) locality (2); and PLYM-132 (2) from W-2 (NFF-5) locality, all British Columbia. All localities in Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Group of *Lymnaea bulimoides* (Lea, 1841)

Discussion.—It is very difficult to consistently separate, by shell only, the many similar morphs found among the groups of *L. bulimoides*, *L. humilis* (Say, 1822), and *L. cubensis* Pfeiffer, 1839.

Environment and Distribution.—Apparently a species of ephemeral ponds, roadside ditches, small, slow streams, usually well vegetated if permanent, bottoms often muddy (Baker, 1911:216, 220; Franzen and Leonard, 1943:405; Clarke, 1973:286–287). Distribution is generally west of the Mississippi River, from British Columbia south to the approximate U. S. / Mexican border, east to Kansas and Louisiana (Hubendick, 1951:fig. 313). In the far west, characteristic of the Columbian and Californian Life Zones (Baker, 1911:211). Geologic range is uncertain, but is previously known at least from late Pliocene (Blancan).

Lymnaea lacerta Pierce, **new species** (Fig. 16.M, 16.N)

Diagnosis.—A small, thin, umbilicate shell with shouldered whorls, a dominant, rugose body whorl and narrowly oval aperture.

Description.—Shell small, thin, of about five regularly and rapidly expanding whorls, body whorl dominant, suture impressed, spire subacute but rather bulbous, nucleus small, ~0.25 mm, nuclear whorls fewer than two, smooth and rounded, subsequent whorls modestly shouldered, with very fine, regularly spaced, near orthocone costellae, ultimate whorl bears broad and low rugae with costellae superimposed, occasionally appearing malleated; aperture narrowly oval, Ha/H ~0.50, outer lip thin, simple, peristome continuous, columellar lip sinuous, weakly plicate, slightly thickened, broadly expanded and folded over, but not hiding, the umbilicus, basal lip joins the columellar lip with a roundly acute angle. Measurements of holotype, an immature specimen: height 4.6 mm; width 2.8 mm; H/W 1.71; Ha 2.25 mm; Ha/H 0.49; whorls 4.25. Largest specimen observed, height >9.0 mm, whorls >5, badly crushed, is from South Ford Creek locality.

Discussion.—*Lymnaea lacerta* is a rather rare component of the lymnaeid fauna of the Kishenehn Basin, being found in small numbers at six localities, and, with the rare exception of the Bowman Creek locality, the thin shell is almost invariably crushed. Among modern lymnaeids, *L. lacerta* resembles *L. cubensis*, several morphotypes of *L. humilis*, and, most closely, the *techella*, Haldeman, 1867, morph of *L. bulimoides*. The latter can be distinguished from *L. lacerta* by its obviously malleated body whorl, lacking rugae, and longer, wider aperture. Fossil lymnaeids of the *bulimoides/humilis* groups, although rather common after the mid-Pleistocene (Kansan) in faunas from the High Plains, are but rarely encountered in strata as old as late Blancan. Older records are, apparently, unknown. The only taxon of similar age that might be confused with *L. lacerta* is Oligocene *L. tumere* Pierce, 1993, from the Cabbage Patch fauna of southwest Montana. *Lymnaea tumere* belongs to the group of *L. stagnalis* Linné, 1758, and can be easily identified by its low, pinched spire, and inflated D-shaped aperture.

Etymology.—Latin, *lacerta*, fem., brawny, with reference to robust outline of this species.

Material.—More than 35 specimens. Holotype: CM 41711 from Bowman Creek (BWN-2) locality, Flathead County, Montana, Coal Creek Member, Kishenehn Formation, middle Oligocene. Additional specimens: KUMIP 289,772 (7) and PLYM-126 from Bowman Creek (BWN-2) locality; PLYM-128 from South Ford Creek (NFF-22) locality; PLYM-127 (15) from Wurtz Bend (NFF-19) locality, all Flathead County, Montana; KUMIP 289,771 and PLYM-129 from Moose City North (NFF-9) locality; CM 41712 (5) and PLYM-130 from W-2 (NFF-5) locality; and PLYM-131 (5) from E-4 (NFF-2) locality, all British Columbia. All localities in Lower Member, Kishenehn Formation, late Eocene-Oligocene.

Class Bivalvia Linné, 1758
 Order Veneroidea H. and A. Adams, 1856
 Family Sphaeridae Dall, 1895
 Subfamily Sphaerinae Baker, 1927
 Genus *Sphaerium* Scopoli, 1777
Type species.—*Tellina cornea* Linné, 1758.
 Subgenus *Sphaerium* s. str.
Sphaerium progrediens Russell, 1952
 (Fig. 16.P–16.R)

Description.—"Shell of moderate size for the genus, almost symmetrical in side view. Beak low on smaller shells, and placed near midlength; in larger shells more prominent, with a forward inclination. Dorsal margins short, sloping from beak; extremities broadly rounded except posteroventral portion, which may be narrowly rounded in less symmetrical examples; ventral margin gently convex. Surface marked by fine, irregular growth lines and on some shells by a growth furrow. Dentition of right valve: one distinct, oblique cardinal tooth, and a toothlike ridge at base of hinge plate; anterior and posterior lateral socket, each with toothlike ridge above and below. Dentition of left valve: two oblique cardinal teeth, separated by a distinct socket, the lower or more anterior tooth having its socket curved upward and backward slightly to constrict opening of socket; one anterior and one posterior lateral tooth, each rising from ventral margin of hinge plate, and each bounded above by a broad longitudinal groove; anterior lateral tooth more prominent, almost pointed" (Russell, 1952:129).

Emmendation.—Valves sub-circular in outline, modestly inflated, walls moderately thick, sculpted with prominent, widely but irregularly spaced, growth furrows (striae), giving appearance of banding, umbonal area smooth, remainder of valve with very fine, closely and more regularly spaced striae between the growth furrows, hinge moderately long and wide, wider at cusps, cusps robust, rounded to slightly angular at top, PIII has a distinct, longitudinal furrow, C3 short, considerably curved, posterior end much heavier. Measurements of hypotype, CM 41715, a right valve: width 9 mm; height 8 mm; thickness 2 mm.

Discussion.—Among modern sphaeriids, *S. progrediens* resembles, in general shape and sculpture, *S. occidentale* Prime, 1860, but differs markedly in strength of sculpture. The growth furrows of *S. progrediens* are stronger, more numerous, and more closely spaced, resulting in a distinctly banded appearance. Among fossil sphaeriids, *S. progrediens* is distinct in shape and in sculpture, and unlikely to be confused with any other except Eocene *S. formosum* (Meek and Hayden, 1856), which, although similar in shape, has much less robust laterals.

Russell's (1952:129) type locality for this species, and for the two unionid taxa he reported from the North Fork of the Flathead River, has been destroyed by erosion.

Environment and Distribution.—Subgenus *Sphaerium* (*s. str.*) is widely distributed across Canada and northern United States. Normal habitat is creeks, rivers and small lakes on mud or sandy mud bottom, usually well vegetated (Herrington, 1962). Geologic range from Upper Jurassic (?) or Lower Cretaceous to Recent (Clarke, 1973:135).

Material.—More than 50 specimens. Figured specimens: CM 41715 from E-4 (NFF-2) locality, and KUMIP 289,774 from W-2 (NFF-5) locality, are both British Columbia. Additional specimens: PSPH-101 (9) from E-5 (NFF-1) locality; PSPH-102 (10) from E-4 (NFF-2) locality; CM 47176 (15) from W-2 (NFF-5) locality, all British Columbia. KUMIP 289,775 (15) from Starvation Bend (NFF-12) locality; PSPH-103 (3) from Wurtz Bend (NFF-19) locality; and PSPH-104 (8) from Bowman Creek (BWN-2) locality, all Flathead County, Montana. All localities in the Lower Member, or the Coal Creek Bed of the Basal Member, Kishenehn Formation, late Eocene-Oligocene.

Subgenus *Musculium* Link, 1807

Type species.—*Tellina lacustris* (Müller, 1774), by subsequent designation (Mörsch, 1862:228, *vide* Clark, 1973:151).

Sphaerium discus Pierce, **new species**
(Fig. 16.S–16.U)

Diagnosis.—A small *Sphaerium* with circular valves, and slightly protruding, weakly calyculate umbones.

Description.—Valves small, circular in outline, inflated, thin, sculpted with fine, closely spaced striae that fade on umbonal region, becoming coarser, stronger, and more widespread as ventral margin is approached, beaks central, protruding, elevated, slightly calyculate, dorsal margin short, sloping sharply from beak, anterior, ventral and posterior margins well rounded, near circular. Lateral teeth are somewhat small and weak. Measurements of holotype, CM 41717, a single right valve: width 3.9 mm; height 4.0 mm; thickness 1.1 mm.

Discussion.—This specimen is so unique that it is difficult to find a species, fossil or living, with which to compare. The produced, slightly calyculate beaks are similar to modern and fossil *S. partumeium* (Say, 1822), common in late Blancan faunas of Nebraska. However, its circular valve outline immediately distinguishes this species from all other sphaeriids.

Etymology.—*discus*—Latin, with reference to the shape of the valve.

Environment and Distribution.—The subgenus *Musculium* is found from Sub-

Arctic Canada and Alaska south through the United States, Mexico, Central America into South America (Burch, 1972), and, locally, in ponds near Flathead Lake, Montana (Elrod, 1902:103). It inhabits almost all types of permanent water, from ponds and lakes to streams with rapid current, generally on mud bottom with some to abundant vegetation, and can be found in apparently seasonal pools. Previously known geologic range is from Miocene to Recent (Clarke, 1973:151–162).

Material.—Five specimens. Holotype, CM 41717, a right valve, and paratype KUMIP 289,777, a partial valve, are from Starvation Bend (NFF-12) locality. Paratypes KUMIP-289,776, a slightly compressed left valve, and CM 41718, a valve fragment, are from South Ford Creek (NFF-22) locality, both localities are in Flathead County, Montana. PSPH-105, a very juvenile valve, tentatively referred to this species, is from E-4 (NFF-2) locality, British Columbia. All localities in Lower Member, Kishenehn Formation, late Eocene-Oligocene.

DISCUSSION

Russell's Fauna.—Surprisingly, despite a rich and diverse fauna recovered, and the depth of this investigation, not all the taxa described by Russell (1952; 1956) were found. Those not found are as follows:

Taxa	Russell's Locality
<i>Triodopsis buttsi</i> Russell, 1956*	E-4
<i>Holospira adventica</i> Russell, 1956	C-2
<i>Ventridens?</i> sp.	C-2
<i>Zonitoides?</i> sp.**	C-2
<i>Physa</i> sp.	C-3
<i>Eliptio salassiensis</i> Russell, 1952	W-1
<i>Lampsilis dayli</i> Russell, 1952	W-1

*—A smaller subspecies was found nearby.

**—May be an incomplete *Polygyroides montivaga* Pierce, 1992.

Nearly all fossil localities investigated by Russell, and during this investigation, are at, or only slightly above, normal stream flow levels for the North Fork. As such, these fossil localities are subject to severe scour by fast, turbulent flow during the strong spring floods, and subsequent slumping of overlying strata, often entirely eroding or covering the exposed fossiliferous bed over a period of a few years. Even within the short time limits of this investigation, major damage to fossil localities are noted, on a year to year basis. From Russell's (1952; 1956) descriptions and photographs, it is apparent that some of his localities now appear very different than when Russell made his collections. Some localities could not be found. For example, W-1 is, apparently, completely destroyed by erosion, and the Coudrey Creek localities (C-2, C-3) are covered by slumping and heavy vegetation. Taxa unique to these localities were not rediscovered. Although our collections from the localities for which we deign to use Russell's designations are probably from within only a few meters of Russell's actual localities, it must be understood that they may not include exactly the same strata collected from by Russell. For example, our collections from the locality referred to as E-4 (NFF-2) comprised 20 taxa, compared to only five taxa collected by Russell (1956:105) from his locality E-4. Even so, our collection includes only two of the taxa he reported from his E-4 locality. Of the remaining three taxa, "*Triodopsis*" *buttsi* was found elsewhere, but only as a much smaller subspecies, "*Binneya*" *antiqua*

was found at adjacent localities upstream, and *Holospira adventica*, which Russell reported here based on fragments only, has not been rediscovered, although fragments of another urocoptid, *Coelostemma dawsonae*, were found at this locality.

The large amount of material collected as part of this investigation permitted correction of some of the taxonomy used by Russell. A list of changes follows:

Russell's taxonomy	New taxonomy
<i>Triodopsis buttsi</i>	= <i>Tozerpina buttsi</i> (Russell, 1956) Ceresidae
<i>Binneya antiqua</i>	= <i>Omalonyx antiqua</i> (Russell, 1956) Succineidae
<i>Anguispira simplex</i>	= <i>Haplotrema simplex</i> (Russell, 1956) Haplotrematidae
<i>Stagnicola newmarchi</i>	= <i>Lymnaea newmarchi</i> (Russell, 1952) Lymnaeidae
<i>Planorbis kishenehnensis</i>	= <i>Biomphalaria kishenehnensis</i> (Russell, 1952) Planorbidae
<i>Gyraulus procerus</i>	= <i>Valvata procerus</i> (Russell, 1952) Valvatidae
<i>Goniobasis</i> sp.	= <i>Tryonia russelli</i> Pierce, n.s. Hydrobiidae

Living species.—Among the surprises encountered in the Kishenehn l.f. were four taxa that could not be distinguished, conchologically, from living taxa. These taxa are as follows:

Discidae	<i>Anguispira</i> sp., cf. <i>A. alternata</i> (Say, 1816)
Ammonitellidae	<i>Polygyrella</i> sp., cf. <i>P. polygyrella</i> (Bland and Cooper, 1861)
Planorbidae	<i>Planorbula</i> sp., cf. <i>P. campestris</i> (Dawson, 1875)
Physidae	<i>Aplexa</i> sp., cf. <i>A. hypnorum</i> (Linné, 1758)

These are not just represented by fragments or by single, deformed shells. The rarest of those above is *Aplexa* sp., cf. *A. hypnorum*, had four good specimens at hand, whereas *Anguispira* sp., cf. *A. alternata* numbered more than 60 specimens, including one very nice specimen lodged in, and cemented into, the aperture of the holotype of *Skinnerelix rothi* (CM-41676) (Fig. 13.B). Despite the fact that the preserved conchological characteristics of these four taxa fall well within the expected range of variation for the modern species, actual biological identity is considered unlikely, and is not implied. However, the habitat preferences and distribution of the modern species were used in studies of sympatry.

Sympatry.—Sympatry is defined, simply, as the natural coexistence of a group of taxa in a given area at a given time. Since climates and environments change with time, the study of the taxa of an ancient fauna or flora can provide valuable clues as to the climate and environment in which they existed. Mollusks, as a result of their low degree of mobility and apparent slow rate of evolutionary change, are excellent indicators of the climate and environment in which they exist. Terrestrial gastropods, especially, closely reflect their environment; in effect, their low mobility means that they are 'stuck with the hand they were dealt.' Unlike mammals, who are highly mobile and migratory, terrestrial gastropods are unable to escape even slow climatic changes. If the climate changes to one beyond their tolerance range, local extinction results. Freshwater mollusks, however, by virtue of their environment, are shielded, at least in part, from the outside terrestrial environment, and are able to survive in isolated suitable microenvironments. For example, cool springs in northern Nebraska harbor taxa adapted to Canadian environments (Taylor, 1960). They are relicts of the Pleistocene.

The rich, diversified, and, at least locally abundant, molluscan fauna of the North Fork Kishenehn Basin clearly indicates a paleoclimate at considerable odds

with the present climate. Since most taxa of the Kishenehn l.f. are extinct, to determine plausible climatic and environmental conditions for the time of deposition of the Kishenehn strata, it was necessary to identify modern analogs of the fossil taxa. It is assumed that the environmental and climatic preferences of these analogous modern taxa will approximate that of the fossil taxa. With these modern analogs, modern areas of sympatry can be established. The climate and environment of these modern areas of sympatry are then used to infer the climate and environment at the time of deposition.

In the case of those four species that are indistinguishable from modern taxa, a modern analog was unnecessary. Several taxa from among the Planorbidae, the Hydrobiidae, and Valvatidae also resembled modern species so closely that the modern species were used as analogs. In some cases, such as *Vallonia kootenayorum*, clearly a member of the living *V. cyclophorella* group, the choice was, again clear. For *Gastrocopta minuscula*, which resembles modern *G. pellucida* (*s. lat.*), and since both are of the same subgenus, the modern species was selected as the stand-in. For a large number of the remaining taxa, the Pupillidae, Planorbidae, and Urocoptidae, and some Helicinidae, those new taxa assignable to modern subgenera were assumed to have the environmental and climatic preferences of the modern subgenus as a whole. In other cases, it was a composite of the requirements of the modern genus that was the best possible match, e.g., *Menetus hilli*, the Oreohelicidae, and the Succineidae. The analogs of the Lymnaeidae were determined by their Group characteristics (see discussion on Groups under Systematics, this paper). In extreme cases, as with the Helicinidae and Ceresidae, it was the composite character of the subfamily or even of the family as a whole that was deemed as the best possible modern analog. Two taxa, *Vertigo doliara*, and *V. micra*, were deemed unsuitable for use in this exercise, since they could not be classified to sub-generic level, and the modern distribution at generic level was too broad to be significant, and the aquatic genus *Tryonia*, imperfectly known, and extinct, was also excluded. Tables 4 and 5 show the analogous taxon selected for each Kishenehn taxon, and the current range of each.

The modern ranges of the analog taxa were mapped. No single area of sympatry for the North Kishenehn Basin l.f., as a whole, was discovered. In actuality, three more or less overlapping areas of sympatry developed: Group I—Tropical Wet environment; Group II—Subtropical semiarid environment; and Group III—Temperate environment. Figures 17 and 18 define the areas of sympatry for Groups I and II. Modern climatic parameters for each of the sympatric areas, as well as for the North Kishenehn Basin, were determined using climatic data available from www.worldclimate.com on the World Wide Web. Although the taxa of the Kishenehn l.f. comprise a broad melange overall with respect to interpreted habitat and environment preferences, they separate naturally into these three climatic groups. In Table 6, the various terrestrial taxa of the Kishenehn fauna are separated into these Groups, with each Group representing a distinct climate preference.

Group I. Tropical, Wet and Dry, Savannah, Aw-As (Köppen, 1931). This Group is comprised of seven terrestrial taxa, five of which have modern analogs restricted to this climate. This Group covers a large area, displaced 25°–40° in latitude South and 15°–55° in longitude East from the Kishenehn Basin. Although the climatic and environmental needs and preferences of the seven members of this group are quite constant, they occupy widely dispersed geographic areas with only *G. pellucida* (*s. lat.*) distributed throughout the total area. Only two of the modern analogs, *G. pellucida* (*s. lat.*) and *Praticolella*, range into other climate groups.

Table 4.—*Analogous terrestrial taxa.*

TERRESTRIAL TAXA	ANALOGOUS TAXA	CURRENT RANGE
CERESIDAE		
<i>Tozerpina buttsi parva</i>	F. Ceresidae	Eastern Mexico
<i>T. lentis</i>	F. Ceresidae	
HELICINIDAE		
<i>Waldemaria monticola</i>	<i>Hendersonia</i>	WI, IA, southern Appalachians
<i>Lucidella salishana</i>	<i>Lucidella/Poeniella</i>	Greater Antilles, Florida Keys, Cent. America & Gulf Coast of Mexico
<i>L. columbiana</i>	<i>Lucidella/Poeniella</i>	
SUCCINEIDAE		
<i>Oxyloma? kintlana</i>	<i>O. effusa</i> Gp.	East of Continental Divide
<i>Omalonyx cocleare</i>	<i>Omalonyx</i>	S. & C. America, Lesser Antilles
PUPILLIDAE		
<i>Pupoides costatus</i>	<i>Ischnopupoides</i>	Four Corners area, Black Hills, & Front Range, CO to NM
<i>P. tephroides</i>	<i>Ischnopupoides</i>	
<i>Gastrocopta miniscula</i>	<i>G. pellucida</i>	Caribbean, Gulf Coast, W. to Baja CA
<i>G. kintlana</i>	<i>Albinula</i>	East of Continental Divide
<i>G. akokala</i>	<i>Albinula</i>	
<i>G. leonardi</i>	<i>Vertigopsis</i>	East of Cont'l Divide, UT-Guatemala
<i>Vertigo consteniussi</i>	<i>Vertigo s.s.</i>	Widespread, Canada, U.S., Mex.
<i>Vertigo, c.f. V. arenula</i>	<i>Vertigo s.s.</i>	
VALLONIIDAE		
<i>Vallonia kootenayorum</i>	<i>V. cyclophorella</i> Gp.	AZ, NM, West TX, Sonora, Chihuahua
HAPLOTREMATIDAE		
<i>Haplotrema simplex</i>	<i>Haplotrema</i>	Coast Ranges of So. CA & Baja CA
UROCOPTIDAE		
<i>Holospira tabrumi</i>	<i>Haplocion</i>	West Texas, Coahuila, Chihuahua
<i>H. beardi</i>	<i>Haplocion</i>	
<i>Coelostemma dawsonae</i>	<i>Coelostemma</i>	Guerrero, Oaxaca, Coahuila, N. Leon
DISCIDAE		
<i>Discus mackenziei</i>	<i>Discus</i>	N. U.S. and S. Canada
<i>Anguispira, cf. A. alternata</i>	<i>Anguispira alternata</i>	E of 97th Meridian & Columbia River
LIMACIDAE		
<i>Deroceras mahiz</i>	<i>D. laeve</i>	Alaska to Central America
<i>D. securis</i>	<i>D. laeve</i>	
ZONITIDAE		
<i>Nesovitrea pulchra</i>	<i>Nesovitrea hammonis</i>	37th parallel N to Arctic Ocean
POLYGYRIDAE		
<i>Praticolella lucifera</i>	<i>P. berlandieriana</i>	Gulf Coast from TX to Yucatan
<i>Ashmunella sp.</i>	<i>Ashmunella</i>	AZ, NM, West TX, & Chihuahua

Table 4.—Continued.

TERRESTRIAL TAXA	ANALOGOUS TAXA	CURRENT RANGE
OREOHELICIDAE		
<i>Oreohelix dawsonae</i>	<i>Oreohelix</i>	S. BC to S. NM
<i>Radiocentrum kintlana</i>	<i>Radiocentrum</i>	S. NM, Chihuahua & Baja CA
AMMONITELLIDAE		
<i>Polygyroidea montivaga</i>	<i>Polygyroidea</i>	Cent. CA
<i>Polygyrella</i> , cf. <i>P. polygyrella</i>	<i>P. polygyrella</i>	OR, WA, ID, MT
HUMBOLDTIANIDAE		
<i>Skinnerelix rothi</i>	<i>Humboldtiana</i>	W. TX thru Cent. Mexico to D.F.
HELMINTHOGLYPTIDAE		
<i>Xerionata constenii</i>	<i>Xerarionta</i>	Coastal CA and Baja California

Table 5.—Analogous aquatic taxa.

AQUATIC TAXA	ANALOGOUS TAXA	CURRENT RANGE
HYDROBIIDAE		
<i>Cincimatia?</i> <i>bowmanana</i>	<i>C. cincimatiensis</i>	ND, UT, Ohio drainage
<i>Fluminicola?</i> <i>calderense</i>	<i>F. fusca</i>	OR
VALVATIDAE		
<i>Valvata procera</i>	<i>V. humeralis</i>	BC, MT, CA, NM, & C. Mex
<i>V. procera spatiosa</i>	<i>V. humeralis</i>	
PLANORBIDAE		
<i>Helisoma triangulata</i>	<i>Helisoma anceps</i>	Canada, U.S., Mexico
<i>Planorbella fordensis</i>	<i>P. subcrenulatatum</i>	YT, MB, MI, CO, CA
<i>Planorbula</i> , cf. <i>P. campestris</i>	<i>P. campestris</i>	BC, MB, NM
<i>Biomphalaria haydeni</i>	<i>Tropicorbis</i>	Gulf States, Mexico, Caribbean
<i>B. spira</i>	<i>Tropicorbis</i>	
<i>B. kishenehnsis</i>	<i>Australorbis</i>	S. & C. America, Lesser Antilles
<i>Menetus textus</i>	<i>Menetus cooperi</i>	CA, AB, AK
<i>M. (M.) hilli</i>	<i>s. gen. Micromenetus</i>	East of Mississippi R, and IA to TX
<i>Gyraulus</i> , cf. <i>G. scabiosus</i>	<i>s. gen. Torquis</i>	AK to Sonora to Cuba
LYMNAEIDAE		
<i>Lymnaea bowmanana</i>	<i>L. palustris</i> Gp.	Holarctic to CA, NM, MO
<i>L. lacerta</i>	<i>L. bulinoides</i> Gp.	W of Miss. R., BC to AZ & NM
<i>L. newmarchi</i>	<i>L. catascopium</i> Gp.	Cent. U.S. & Canada & BC to CA
PHYSIDAE		
<i>Aplexa</i> , cf. <i>A. hypnorum</i>	<i>A. hypnorum</i>	Holarctic to WA, CO, OH, MD
BIVALVES		
SPHAERIDAE		
<i>Sphaerium progrediens</i>	<i>Sphaerium</i>	Canada & U.S. north of 37°N
<i>S. (M.) discus</i>	<i>s. gen. Musculium</i>	Canada & U.S.



Figure 17.—Group I Area of Sympatry.
---*Gastrocopta pellucida* (s.l.) salient.

The multiple sub-centers of sympatry for these taxa are as follows: The Antilles (Caribbean) (4 taxa); eastern San Luis Potosi, Mexico (3 taxa); Yucatan Peninsula (2 taxa); and northern South America (2 taxa). In common, these taxa require, or at least tolerate, a very constant tropical climate: MAT 25°–27°, Annual Range 3°–10°C, Annual Precipitation >100 cm, and seasonally winter dry (www.worldclimate.com), and are generally found at relatively low elevations.

Group II. Subtropical/Tropical Semiarid/Arid, Bsh-Bwh, Cs. The composite ranges of the 17 terrestrial taxa in this group cover a broad area the Southwestern United States and Mexico, from the Gulf Coast to the Colorado River and Baja California, with three distinct sub-centers. However, climatic data determined that the three *foci*, East, Central and West, had enough climatic parameters in common to be treated broadly as a single sympatric area, despite the rather large longitudinal separation between the individual centers. These taxa are displaced 16°–33° in latitude South and in longitude from straight south to 7°–14° East. In Table 6, Group II is shown split into its sections. An Eastern section, IIE, composed of 5 taxa, is centered in eastern Coahuila and Nuevo Leon. For this section, IIE, the climate and environment of Monterrey, Nuevo Leon, Mexico is a good approximation: MAT 22°C, Annual Range 13.5°C, Annual Precipitation 61 cm, and seasonally winter dry, with terrain elevations of ~500 m. A Central section, IIC, composed of 12 taxa, centers in the lower Rio Grande Valley of New Mexico, and adjacent Chihuahua, and is generally representative of the Southwestern Mol-



Figure 18.—Group II Area of Sympatry.
 --- *Gastrocopta pellucida* (s.l.) salient
 *Praticolella berlanderiana* salient
 - - - - *Ischnopupoides* salient

luscan Province (*sensu* Henderson, 1931:182). For this Central section, IIC, the suggested climate and environment would be an average of that occurring at Elephant Butte Reservoir, NM and Winston, NM, to include the different elevations encountered. MAT ranges from 11.3°C to 15.6°C, Annual Range 19.5°C to 22°C, Annual Precipitation 24–32 cm, seasonally winter dry and with terrain elevations from 1,400–2,000 m. In general, IIC is drier and at a greater elevation than IIE. The Eastern and Central sections, although different geographically, are fairly similar with regards to climate, and quite similar when the climates are adjusted for differences in elevation. However, only three taxa are in common, the widespread and tolerant *G. minuscula* and the two *Holospira*. The Western section, IIW, is composed of five taxa that have been displaced almost exactly south to a center of sympatry in southern California and Baja California, a displacement of some 16° to 17° of latitude (~1,800 km). This section includes the isolated western band of the genus *Radiocentrum*, the eastern band of which occurs in section IIC, the genus *Ashmunella*, also found Group IIC, and the seemingly ubiquitous *G. pellucida*. These taxa seem well adapted to a summer dry climate, Mediterranean, with MAT 14°–18°C, Annual Range 10°–14°C, Annual Precipitation 36–56 cm, and at moderate elevations, generally less than 1,000 m.

Group III. Humid Subtropical/Humid Continental, Ca, Da. Group III, the Temperate climate group, is composed of 15 terrestrial taxa whose modern analogs

Table 6.—*Kishenehn l.f., terrestrial environmental groups.* () = *Cabbage Patch fauna taxa*; W = *Western distribution only.*

TERRESTRIAL TAXA	Humid Tropi- cal Aw, As	Dry Tropical/Sub Trop			Temperate	
	Group I	BSh-BWh	Group II	BSh-Cs	Caf-Daf Group III	BS
		E	C	W	Humid	Dry
CERESIDAE						
<i>Tozerpina buttsi parva n.s.</i>	X					
<i>T. lentis n.s.</i>	X					
HELICINIDAE						
<i>Waldemaria monticola</i>					(X)	
<i>Lucidella salishora n.s.</i>	X					
<i>L. columbiana n.s.</i>	X					
SUCCINEIDAE						
<i>Oxyloma? kintlana n.s.</i>					X	
<i>Omalonyx cocleare n.s.</i>	X					
PUPILLIDAE						
<i>Pupoides costatus n.s.</i>			X			
<i>P. tephroides</i>			X			
<i>Gastrocopta miniscula</i>	X	X	(X)	X		
<i>G. kintlana n.s.</i>					X	
<i>G. akokala n.s.</i>					X	
<i>G. leonardi</i>			(X)			
<i>Vertigo consteniusi n.s.</i>			X		X	
<i>V. cf. V. arenula</i>			X		(X)	
VALLONIIDAE						
<i>Vallonia kootenayorum n.s.</i>			X			W
HAPLOTREMATIDAE						
<i>Haplotrema simplex</i>				X		
UROCOPTIDAE						
<i>Holospira iabrumi n.s.</i>		X	X			
<i>H. beardi n.s.</i>		X	X			
<i>Coelostemma dawsonae n.s.</i>		X				
DISCIDAE						
<i>Discus mackenziei</i>					X	
<i>Anguispira, cf. A. alternata</i>					X	
LIMACIDAE						
<i>Deroceras mahiz</i>					(X)	
<i>D. securis</i>					(X)	
ZONITIDAE						
<i>Nesovitrea pulchra</i>					(X)	
POLYGYRIDAE						
<i>Praticolella lucifera n.s.</i>	X	X				
<i>Ashmunella sp. n.s.</i>			X	X		
OREOHELICIDAE						
<i>Oreohelix dawsonae n.s.</i>						W
<i>Radiocentrum kintlana n.s.</i>			X	X		
AMMONITELLIDAE						
<i>Polygyroidea montivaga</i>						(W)
<i>Polygyrella, cf. P. polygyrella</i>						W
HUMBOLDTIANIDAE						
<i>Skinnerelix rothi n.s.</i>			X			
HELMINTHOGLYPTIDAE						
<i>Xerionata constenii n.s.</i>				X		

are yet living in the United States and southern Canada. All but four of the analogs of the Group III taxa have been displaced eastward, and are typical of the Eastern Division mollusks (*sensu* Henderson, 1931:182). For these, a center of sympatry would approximate the State of Kentucky, with a climate ranging from Humid, Continental, to Humid, Subtropical, with warm summer. Climatic data for Lexington, Kentucky, with possible ranges to include the entire best area of sympatry, are as follows: MAT $12.7^{\circ} \pm 5^{\circ}\text{C}$, Range 25° – 30°C , Annual Precipitation ~ 100 cm, little or no dry season, and at moderate elevations of less than 1,000 m. Two of the four terrestrial analogs that are western in modern distribution, occupy a climatic region quite similar to the eastern taxa. *Polygyroidea* is now found at the edge of the Group IIW area in its tiny refugium at moderate altitude in the central Sierra Nevada, where the climate is about 6°C warmer than Montana's Flathead Valley, but with about twice the rainfall. *Polygyrella* is now found only on isolated mountainous areas having greater than normal rainfall (rainfall windows of Roth and Emberton, 1994), in eastern Oregon, Washington, Idaho, and western Montana. The genus *Oreohelix* and the *Vallonia cyclophorella* Group are Western Division (*sensu* Henderson, 1931:182) taxa that can tolerate somewhat drier environments than the remainder of this group. The *Vallonia cyclophorella* Group has isolated distribution in the East.

Six of the terrestrial taxa of Group III, two of Group IIC, and one aquatic taxon are members of the late Oligocene-early Miocene (Arikareean) Cabbage Patch fauna of southwestern Montana (Pierce and Rasmussen, 1992; Pierce, 1992; 1993). The proposed climatic preference of the Cabbage Patch fauna was: MAT $>10^{\circ}\text{C}$, January mean temperature $\geq 5^{\circ}\text{C}$, July mean temperature 15° – 20°C , precipitation ≥ 50 cm, and elevation >800 meters (Pierce, 1993:990). This is quite compatible with the modern climate suggested above for Group III.

The aquatic taxa of the Kishenehn fauna (Table 7) have a more western flavor (8 of 19 taxa), and the majority suggest cool water and a temperate climate. *Cincinnatia* is considered western, with its nearest modern verifiable occurrence nearly 700 km south, and because its sister species, *Fonticella*, is exclusively western. For aquatic taxa, east/west dispersion, across existing drainage divides, is difficult. North/south dispersion, generally along drainages and flyways, is more common, e.g., the type locality of *Valvata humeralis*, a common, low altitude northern taxon, is in cool high altitude lakes of central Mexico (*vide* Bequaert and Miller, 1973:213). Due to this shielding effect of water, climatic data derived from cool freshwater taxa can be misleading. Data derived from taxa requiring warmer waters is more reliable, and informative. *Biomphalaria glabrata* (subgenus *Australorbis*), the modern analog of *B. kishenehnensis*, is incapable of reproduction with water temperatures below 20°C , and water temperatures as low as 5°C result in death within a week (Taylor, 1985:269). *Biomphalaria havanensis* (subgenus *Tropicorbis*), analog for *B. haydeni* and *B. spira*, is presently not found north of 30° North Latitude, which is approximately coincident with the January Mean Temperature isotherm of 10°C .

Environmental data derived from freshwater taxa can be useful. From the environmental data suggested by the modern analogs of these taxa, a picture emerges of highlands surrounding or paralleling a valley containing a chain of lakes, some large, some small, some sandy, some mud bottomed, interconnected by a slow-flowing river and or streams, and subject to seasonal flooding and transient ponds, with permanent and semi-permanent water, generally well vegetated to locally almost overwhelmed by vegetation and marshy, but retaining some rocky littoral

Table 7.—*Kishenehn l.f., aquatic environmental groups. W = Western distribution.*

AQUATIC TAXA	Tropical Jan. Mean > 20 C	Subtropical Jan. Mean > 10 C	Temperate
HYDROBIIDAE			
<i>Cincinnatia? bowmanana n.s.</i>			W
<i>Flumicola? calderense n.s.</i>			W
VALVATIDAE			
<i>Valvata procera</i>			W
<i>V. procera spatiosa n.ss.</i>			W
PLANORBIDAE			
<i>Helisoma triangulata n.s.</i>			X
<i>Planorbella fordensis n.s.</i>			X
<i>Planorbula, c.f. P. campestris</i>			W
<i>Biomphalaria haydeni</i>	X	X	
<i>B. spira n.s.</i>	X	X	
<i>B. kishenehnsis</i>	X		
<i>Menetus textus. n.s.</i>			W
<i>M. (M.) hilli n.s.</i>			W
<i>Gyraulus, c.f. G. scabiosus</i>			X
LYMNAEIDAE			
<i>Lymnaea bowmanana n.s.</i>			X
<i>L. lacerta n.s.</i>			W
<i>L. newmarchi</i>			X
PHYSIDAE			
<i>Aplexa, c.f. A. hypnorum</i>			X
BIVALVES			
<i>Sphaerium progrediens</i>			X
<i>Sphaerium (M.) discus n.s.</i>			X

areas. An earlier warm water episode is suggested by the *Biomphalaria* spp. *Biomphalaria kishenehnsis*, clearly a member of the subgenus *Australorbis*, is a rare component requiring tropical conditions and is, apparently, found only low in the section. Seasonal fluctuation of water levels is suggested by the *Biomphalaria* spp., *Lymnaea lacerta*, and *Aplexa hypnorum*, all of which are quite tolerant of desiccation.

Extralimitality—Terrestrial Taxa.—The molluscan fauna of the early-middle Tertiary of western North America, especially in western Montana where four diverse and significant faunas have now been studied, are notable for an unusual extralimitality of the faunas (Table 8). Genera, subfamilies, even families that are now distributed in widely divergent parts of North America, the Caribbean region, South America, and even Asia are found here in sympatric association during the Tertiary. The cause of this current extralimitality is in major changes in climate, cooling and drying, which occurred during and after the Eocene in the Western Interior of North America, most notably, the Middle Eocene Event (Berggeren and Prothero, 1992; Retallack, 1992; Wolfe, 1992). Since the climate has changed, the modern fauna has changed to adapt to the new climate.

Taxa displaced longitudinally, i.e., predominantly East/West, are, usually, so displaced by a change in moisture regimes that no longer meet the requirements of the taxa. As a general rule in North America, isohyets [lines depicting equal Mean Annual Precipitation (MAP)] increase eastward from the Rocky Mountains.

Table 8.—*Extraterritoriality of terrestrial faunas.*

Local fauna (l.f.)	NALMA	Usable taxa		Displacement		Reference
		None	Latitudinal	Longitudinal		
Flint Creek l.f. Granite Co., MT	e. Barstovian?	2 100%		2 100%		Pierce & Rasmussen, 1989
Cabbage Patch l.f. Granite & Powell Co's., MT	Arikarean	16 100%	8 63%	3 29%	5 31%	Pierce & Rasmussen, 1992 Pierce, 1992; 1993
Deep River l.f. Meagher Co., MT	Orellan-Arikarean	11 100%	5 45%	4 36%	2 18%	Roth & Emberton, 1994
Kishenehn l.f. Flathead Co., MT & So. Br. Col.	Chadronian-Arikarean	33 100%	13 39%	18 55%	2 6%	Russell, 1952; 1956 This paper
White River l.f. Douglas area, WY	Group III	15/100%	13/87%	0	2/13%	
Three Forks l.f. Jefferson & Gallatin Co's., MT	Group II	11/100%	0	11/100%	0	
	Group I	7/100%	0	7/100%	0	
	Chadronian-Orellan	12 100%	3 25%	6 50%	3 25%	Evanoff et al., 1992
	Uintan-Chadronian	8 100%	4 50%	4 50%	0 0	Roth, 1986

West of the Rocky Mountains, local conditions dominate in determining MAP. For example, although it is generally quite dry between the coastal ranges of western North America and the Rocky Mountains, some intervening mountainous areas often receive much greater precipitation, becoming "rainfall windows" (Roth and Emberton, 1994), and are *refugii* of small size for certain moisture limited taxa. The two Ammonitellidae encountered as fossils at several of these Montana localities serve as examples. *Polygyrella polygyrella* (Three Forks l.f., White River l.f., and Kishenehn l.f.) now exists in only a few small, isolated, colonies in mountainous areas from the Bitterroot Mountains of Idaho/Montana to the Blue Mountains of eastern Oregon/Washington (Pilsbry, 1939:559). *Polygyroidea harfordiana* (modern analog for *P. montivaga*, Cabbage Patch l.f. and Kishenehn l.f.) now inhabits only a small, stenotropic area of higher precipitation, ~100 cm MAP, near Yosemite National Park (Pilsbry, 1939:566). Other moisture limited taxa are now found in areas, east or west, where favorable conditions are regional in extent, e.g., the modern analog of the subfamily Hendersoninae (Helicinidae), represented by several species from the Kishenehn, Deep River, and Flint Creek local faunas, has been displaced eastward. Once widely dispersed over the central United States, at the present time, the modern analog, *Hendersonia occulta*, has two loci; the first extending from central Iowa to the Upper Peninsula of Michigan, representing post-glacial dispersal from the unglaciated *refugium* of Iowa and Wisconsin; and the second in the central and southern Appalachians (Hubricht, 1985:map 1). This points up the problem of defining whether a specific taxon is now extralimital, or is considered endemic. If those taxa still encountered in the general area (within 320 km) are considered endemic, *Polygyroidea harfordiana* would be extralimital, whereas *Polygyrella*, cf. *P. polygyrella*, still found within 320 km of the Kishenehn Valley, would be endemic. In the case of the Kishenehn l.f., all temperate aquatic gastropods and all but two of the Group III terrestrial taxa can yet be found nearby (within 320 km), often just across the Continental Divide, and, from that standpoint, are, herein, considered endemic. However, many of these taxa are so found on the fringe of their present range, and exist only in sometimes isolated microenvironments. Therefore, if defined on the core of their present range, most of these taxa are extralimital.

Latitudinal displacement of taxa, i.e., on a North/South line, is due, usually, to cooling, or warming, of climates, and can be rather more complex. Modern climatic patterns tend to interpose a low precipitation belt of steppe to desert aspect at mid-latitudes in the western and central portions of continents (cf. Finch et al., 1957:123–127). Latitudinal displacements south from the western Montana origin of the faunas considered herein have, inevitably, to enter, or even cross, environments much drier than their origin. Taxa forced to retreat south due to a cooling climate but that yet require a relatively humid regional climate will actually have to retreat diagonally to the southeast.

Table 8 compares the degree of extralimitality displayed by each of the six mid-Tertiary faunas characteristic of the Western Interior Basin. As might be expected, the degree of extralimitality varies with age of the fauna, with the older faunas including as many as 50% extralimital taxa. Endemicity (not displaced) reflects an opposite trend, becoming greater among the younger faunas. However, the difficulty in defining whether a given taxon is endemic or longitudinally extralimital can manipulate the results. The Kishenehn l.f. is presented both as a whole and as three individual climatic groups. Note that all of the Group I and II analog taxa utilized in this comparison are extralimital, displaced south, while

87% of the Group III are endemic, based on the modern analog taxa being encountered within 320 km of the Kishenehn Basin.

The seven taxa of Group I are now unevenly spread across a wide area of the Caribbean basin, extending from Eastern Mexico to Antiqua. Although diagonal displacements are variable, the latitudinal displacement for six of the seven taxa is a rather constant 25°–27° in latitude (<3,000 km). The genus *Omalonyx* is an almost unknown factor, since so little has been published on it. Other than Thiele's (1992:801) assertion, I find no record of this genus in Central America. Group I taxa are a blend of taxa currently occupying the Caribbean Basin and well adapted to the wet tropical climate that is characteristic of the area. The Group I taxa establish a base level climate for this part of the Continental Western Interior during the middle Tertiary.

Group II is separable into three sections. The eastern section (IIE) is composed of gastropods characteristic of the interior of the Gulf Coastal Plain of Mexico and southern United States, and are displaced southward by 20° to 30° (~2,200–3,300 km). The central section (IIC), representative of the Southwestern Molluscan Province (*sensu* Henderson, 1931:182), and the western section, Group IIW, representative of the Californian Molluscan Province (Henderson, 1931:183) are composed of gastropods whose modern climatic tolerances are very similar. These Groups are displaced southward by 15° to as much as 25° of latitude (~1,650 to 2,750 km). The Group II taxa are the result of a major shift in climate to drier and slightly cooler parameters.

In comparison, Group III taxa have been dispersed longitudinally, and include taxa whose modern analogs (13 of 15 terrestrial taxa) may still be found in the general vicinity (within some 320 km) of northwestern Montana, although when so found are, usually, at the limit of their normal range. In a very broad sense, these taxa must be considered endemic, although the center of their modern distribution may be distant. Among the terrestrial taxa of Group III, all but three (12 of 15 taxa) belong in Henderson's Eastern Molluscan Division (*op. cit.*, p. 180). Although widely dispersed now, these taxa were, in the more recent past and during periods of more equitable climate, even more widely spread. This is additional confirmation of the observation by Roth and Emberton (1994:103) "that their modern absence from the western interior is a derived, rather than primitive, state." The Group III taxa represent a further shift in climate to cooler but wetter parameters than found during Group II time.

Extralimitality - Aquatic Taxa.—Aquatic mollusks are shielded from the extremes of the environment outside their water habitat, and may not be representative of the outside environment. Of the 19 aquatic taxa found in the Kishenehn sediments, 16 are temperate cool water taxa, equally divided between modern eastern and western distribution. The remaining three taxa encountered are characteristic of warm waters, and are known to require certain minimum water temperatures to sustain life and/or reproduction. As previously noted, *Biomphalaria glabrata* (Say, 1818), a most plausible modern analog for *B. kishenehnsis* and subgenus *Australorbis*, must have water temperatures of 20°C or more to reproduce. *Biomphalaria havanensis* (Pfeiffer, 1839), an equally plausible modern analog of *B. haydeni* and *B. spira*, and the subgenus *Tropicorbis*, can tolerate somewhat cooler water, but is not found where January Mean Temperatures fall below 10°C. In each case, a minimum temperature can be established, suggesting that tropical temperatures existed (Group I) for *B. kishenehnsis* and at least subtropical

Table 9.—Correlation of Kishenehn Group II fauna. Number of species in l.f. as indicated. X indicates subgenus uncertain. Cd(Kishenehn l.f. <> White River l.f.) = 94.7%; Cd(Kishenehn l.f. <> Three Forks l.f.) = 67.0%; Cd(Three Forks l.f. <> White River l.f.) = 62.5%.

TERRESTRIAL TAXA	Taxa in common		
	Kishenehn l.f.	Three Forks l.f.	White River l.f.
PUPILLIDAE			
<i>Pupoides (Ischnopupoides)</i>	2	3	1
<i>Gastrocopta (Albinula)</i>	2	2	
G. other s.sp.	2	1	X
VALLONIIDAE			
<i>Vallonia (Cyclophorella) Gp)</i>	1		X
UROCOPTIDAE			
<i>Holospira (Haplocion)</i>	2		X
POLYGYRIDAE			
<i>Ashmunella sp.</i>	1		1
OREOHELICIDAE			
<i>Radiocentrum sp.</i>	1	1	1
AMMONITELLIDAE			
<i>Polygyrella, cf. polygyrella</i>	1 ^a	1	1
HUMBOLDTIANIDAE			
<i>Skinnerelix sp.</i>	1		1
HELMINTHOGLYPTIDAE			
<i>Xerionata sp.</i>	1		1

^a Modern analog from Group III.

temperatures (Group II) for *B. haydeni/spira*. Both modern *Biomphalaria* are quite tolerant of seasonal desiccation.

Correlation of faunas.—As was previously noted, the mid-Tertiary molluscan faunas of the Western Interior of North America are becoming fairly well known and understood. Within the last 50 years, six molluscan local faunas (l.f.) have been described (Table 8), beginning with Russell's (1952; 1954) first studies of the Kishenehn Basin. Faunal correlations among these l.f. should result in some insight as to their relative ages. The Kishenehn l.f. is unique in that it is composed of molluscan groups representing the three distinct climatic environments that, apparently, for a short period of time, coexisted temporally in separate, but nearby, geographic environments. For correlation, each Kishenehn l.f. molluscan climatic group was compared with the remaining Western Interior l.f. It was immediately apparent that the Group I mollusks, representing a wet tropical environment, were unique. Except for the broadly tolerant *Gastrocopta minuscula*, the remaining taxa are unknown among the other l.f. Group II taxa, indicative of a tropical to subtropical semiarid environment, correlate well with both the Three Forks l.f. and the White River l.f. Correlations are based upon a modified Coefficient of Dice (Cd) (Sneath and Sokal, 1973:131). It is modified to measure similarities among the three or more faunas used in each study, and is based not on the total taxa of each fauna, but upon the taxa of the three or more faunas that are shared by two or more of the faunas within the designated group. The Three Forks l.f. and White River l.f. fell within the group based on The Kishenehn l.f. group II mollusks (Table 9). Correlation indices from this triplet are as follows:

Table 10.—Correlation of Kishenehn Group III fauna. Number of species in l.f. as indicated. Cd(Kishenehn l.f. <> Cabbage Patch l.f.) = 84.6%; Cd(Kishenehn l.f. <> Deep River l.f.) = 69.6%; Cd(Cabbage Patch l.f. <> Deep River l.f.) = 50.0%.

TERRESTRIAL TAXA	Taxa in common		
	Kishenehn l.f.	Cabbage Patch l.f.	Deep River l.f.
HELICINIDAE			
<i>Waldemaria monticola</i>	1	1 ^a	
<i>Hendersonia</i> sp.		1 ^a	1
PUPILLIDAE			
<i>Pupoides (Ischnopupoides)</i>	2	1	1
<i>Gastrocopta (s. str.)</i>	1	1	
<i>G. (Albinula)</i>	2	3 ^b	1
<i>G. (Vertigopsis)</i>	1	3	
VALLONIIDAE			
<i>Vallonia (Cyclophorella Gp.)</i>	1		1
DISCIDAE			
<i>Discus</i> sp.	1		1
<i>Anguispira</i> sp.	1		1
LIMACIDAE			
<i>Deroceras mahiz</i>	1	1	
<i>Deroceras securis</i>	1	1	
ZONITIDAE			
<i>Nesovitrea pulchra</i>	1	1	
OREOHELICIDAE			
<i>Oreohelix</i> sp.	1	1	1
<i>Radiocentrum</i> sp.	1		1
AMMONITELLIDAE			
<i>Polygyroidea montivaga</i>	1	1	

^a From Flint Creek l.f. (Pierce & Rasmussen, 1989).

^b As subgenus *Ameralbinula*.

Kishenehn Gp. II l.f. to White River l.f.—94.7%

Kishenehn Gp. II l.f. to Three Forks l.f.—67.0%

Three Forks l.f. to White River l.f.—62.5%

A second comparison was made using the taxa of Kishenehn Gp. III l.f., including several taxa that could tolerate both Gp. II and Gp. III climatic conditions. It was found that the Cabbage Patch l.f. and the Deep River l.f. (Table 10) had significant correlation indices with the Kishenehn l.f.:

Kishenehn Gp. III l.f. to Cabbage Patch l.f.—84.6%

Kishenehn Gp. III l.f. to Deep River l.f.—69.6%

Cabbage Patch l.f. to Deep River l.f.—50.0%

Based on these correlations with and among the relatively well-dated molluscan l.f. of the Western Interior, it can be determined that the Kishenehn Gp. II l.f. could represent ages as old as Uintan or as young as Chadronian, with a Duchesnean-Chadronian age most probable. Kishenehn Gp. III l.f. could range from Orellan to early Barstovian with an Orellan-Arikareean age most probable. The Kishenehn Gp. I l.f. remains enigmatic, in that it bears no resemblance to any other mid-Tertiary fauna of the Western Interior. The tropical, moist climate necessary for these mollusks must have predated the semiarid climate of the late

Duchesnean-Chadronian Ages, and would, most probably, represent the Uintan to early Duchesnean.

Conclusions.—The molluscan fauna of the North Fork Kishenehn Basin presents several most interesting problems. This fauna can be clearly separated into three distinct climatic groups, e.g., I. Tropical, Wet; II. Tropical-Subtropical, Semi-arid; and III. Temperate, Moist. However, taxa representing Tropical and Temperate groups can be found closely associated in the same level at several of the localities. On the face of it, this appears paradoxical, but on examination, three scenarios need to be examined:

Scenario 1. The taxa of all three climatic groups did, in fact, coexist in the same area at the same time. However, in examining the taxa involved, and their modern analogs, it becomes apparent that the climates required for many of the taxa are mutually exclusive. For example, it would be most unlikely for a wet tropical-adapted *Lucidella* or *Omalonyx* to survive in the moist temperate climate occupied by the Ammonitellidae. Accordingly, this scenario is rejected.

Scenario 2. The three climatic groups are separated by time, and represent a history of climatic change for this area and time. As such, an upward progression on outcrop from Group I (low) to Group III (high) would be expected. This is not what was observed. For example, in the lowest units of Locality CMC-1, a robust assemblage of Helicinidae, Ceresidae, and *Omalonyx* (all Group I) are found associated with *Polygyrella* c.f., *P. polygyrella*, *Nesovitrea pulchra*, and two species of albinulid *Gastrocopta* (all Group III). However, at most localities, there is a general tendency for Group I taxa to be concentrated in lower strata, disappearing upwards, and for the diversity and abundance of specimens of Group III to increase upwards, becoming dominant to exclusive near the top at several localities.

The evidence observed at any given locality suggests that sedimentation was rapid, probably involving seasonal depositional episodes, and without significant breaks, either of nondeposition or erosion. In fact, unconformities, mature paleosols, and faults are not found at any outcrop. Thus, the time interval represented by any given outcrop is, geologically, brief. This agrees well with the findings of Tabrum et al. (1996:307) that, in southwest Montana, most of these intermontane sequences are of limited time span, and, although thousands of feet thick, most are shorter than a million years in duration. In addition, the North Fork of the Flathead River is a strike river. It flows longitudinally through the basin, staying near the axis of the basin, and erodes only the sediments from near the top of the Lower Member of the Kishenehn Formation. Since nearly all localities are a result of erosion by the river, all those localities designated by a NFF symbol (see Figs. 2, 4) are, therefore, of approximately the same age. This suggests that only a limited time interval is recorded by all these localities (Fig. 4). Localities along the tributaries of the North Fork, which tend to enter the river at near right angles, are time transgressive. Localities on tributaries from east of the river are younger, while those from west of the river are older. Unfortunately, these localities are few, and only on the east side of the river. Those along Bowman Creek and Kintla Creek are, indeed, younger based on mollusks and/or vertebrates. The Kishenehn Creek locality, KSH-1, based on cf. *Oligoryctes* sp. only, could be as young as Orellan. There were no localities on tributaries entering from the west reported herein. However, review of taxa reported by Russell (1952; 1956) from along Coudrey Creek (his C-1 to C-3) in British Columbia, strongly suggest that this

fauna is from a warmer climate and older age (since it includes *Biomphalaria kishenehnsis*, Group I).

The climatic cycles of the Eocene/Oligocene are fairly well known (cf. Prothero, 1994; Wolfe, 1992). There were intervals during the Eocene during which climatic change, usually cooling, were rapid and dramatic. A notable cooling event occurred in the middle Eocene (probably middle Duchesnean) (Prothero and Emry, 1996); a second occurred just past the Eocene/Oligocene border, the "Terminal Eocene Event" of Wolfe (1978). It may be possible that a mature, diverse temperate fauna could totally replace a tropical fauna during so short a time interval, but not likely. However, the paradox of tropical and temperate species coexisting in the lower strata of these localities is not resolved.

Scenario 3. The three climatic groups represent lowland and upland taxa existing at about the same time but separated by only moderate distance. Early contractile movement along the Lewis Thrust resulted in bold mountains, the ancestral Clark, Lewis, and Livingston Ranges, east of the present Kishenehn Basin area. In these mountains, a mature, diverse temperate gastropod fauna could have had time to develop. Later, as extensional movement began along the Flathead and other faults, asymmetric basins developed on the west flank of the ancestral Clark Range. Oxygen isotope studies (D. Dettmann, written communication, 1997) have suggested a meltwater contribution to the Eocene Kishenehn lakes; the runoff from a seasonally snow-capped ancestral Livingston Range would be a most plausible source. In the lowlands to the west of the mountains, a Tropical fauna characteristic of the early Eocene Western Interior could linger on as a relict fauna in these well-watered *refugii*, despite some cooling and decreasing precipitation, relying on the runoff waters for survival, while the Subtropical, Semiarid dry woodland (Retallack, 1992:382) fauna developed on adjacent, drier slopes. In the case of the Kishenehn Basin, paleocurrent studies indicate the ancestral Clark and Livingston Ranges were the primary source of sediment and runoff, resulting in a large, seasonally variable lake or chain of lakes, capable of sustaining wet-tropical vegetation, but surrounded by a semiarid, dry woodland terrain. The Temperate fauna (Group III) was, initially, transported into the basin from the eastern mountains. The empty shells of many terrestrial gastropods, such as the pupillids and vallonids, are known to be superb floaters, difficult to sink even in turbulent water. Larger taxa, such as the ammonitellids, may have been washed in with some body parts intact, resulting in more or less neutral buoyancy. In any event, these shells could arrive with little evidence of abrasion, and would tend to be deposited in windrows along the shorelines of the seasonally fluctuating lake(s). The end climate after the "Terminal Eocene Event" could no longer support the Tropical and Subtropical faunas in the lowlands, but they could have been replaced rapidly by the Temperate fauna that already existed in the nearby highlands.

The assumptions from Scenario 2 that deposition was rapid and nearly continuous, that the strata encountered vary in age from oldest near the SW margin of the basin to youngest near the NE margin, and the prejudicial effect of a strike river tending to expose sediments of similar age, are all valid constituents of Scenario 3. Considering the paleotopography known for this area, this scenario is plausible. By early Eocene, at the termination of the contractile stage of tectonics, regional topography resembled a regionally-reversed version of the modern northern Amazon Basin/Andes Mountains. The difference in latitudinal wind flow, from the northeast to southwest pattern characteristic of near equatorial north

latitudes, to the northwest to southeast flow consistent with latitudes of 40°–50° north latitude, would result in ample precipitation to maintain a Tropical wet environment (Amazon Basin analog) west of the well-watered ancestral Continental Divide mountains (Andes analog). The dramatic climatic changes caused by the global cooling episode at the end of the middle Eocene, the Middle Eocene Event (middle Duchesnean, ca. 37–38 Ma) (Prothero and Emry, 1996) severely curtailed tropical and warm adapted taxa of the Western Interior. Possible uplift farther to the west, concurrent with the early extensional phase of tectonics (mid-Eocene), would lead to decreased precipitation in the wet tropical terrain west of the mountains, resulting in the semiarid dry woodland environment of the late Eocene. Further severe cooling during the “Terminal Eocene Event” led to the extinction of the Group I and II faunas at the lower elevations of the Kishenehn Basin, and replacement by the Temperate Group III fauna from the eastern highlands.

Even after this relatively detailed study of the northern Kishenehn Basin, an exact age cannot be unambiguously determined. The single radiometric date of 33 ± 1 Ma only establishes a minimum age for the Commerce Creek area, and coincides, approximately, with the “Terminal Eocene Event.” Younger sediments should occur as the footwall boundary is approached. Fossil mammals in association at molluscan localities are limited. Those from nearby mammal localities are few but do provide approximate dates. The North American Land Mammal “Ages” shown on Figure 2 at several localities were provided by M. Dawson (personal communication, 1999) and are, admittedly, preliminary. The NFF 12 locality is dated as ?Duchesnean-Chadronian based upon cf. *Procaprolagus*. The KSH 1 mammal locality age, labeled as ?Chadronian-Orellan, is based on a specimen of cf. *Oligoryctes*. The youngest date, early Arikareean (late Oligocene) for KTL 3 is based on *Pacculus* sp. These dates do show a definite trend for younger strata on the eastern side of the basin.

The probable ages of the Group II and Group III faunas of the Kishenehn Basin (see Correlation of Faunas, above) fit quite well into that scenario. The Group II fauna, which correlates extremely well to the White River l.f., existed in the lowlands west of the mountains during the Chadronian NALMA (post-Middle Eocene Event–pre-Terminal Eocene Event). The Group III taxa, correlating very well to the Arikareean Cabbage Patch l.f., which began to appear near the base of the exposed Kishenehn stratigraphic section during the Chadronian NALMA, is an upland fauna that colonizes and becomes dominant in the lowlands during the late Chadronian-Orellan NALMA's, replacing Groups I and II faunas, and is the precursor of the typical Arikareean NALMA fauna of the Western Interior, as typified by the Arikareean Cabbage Patch fauna of southwestern Montana. The Group I taxa, which are unique, are probably typical of the Tropical Uintan-Duchesnean (pre-Middle Eocene Event), and had persisted as a relict fauna in isolated suitable environments of the western lowlands into the Chadronian NALMA.

The complete absence of unionid clams from the strata studied is notable. Russell (1952:125–128; 1955:105) found two unionid species, *Elliptio salissiensis* Russell, 1952 and *Lampsilis dayli* Russell, 1952 at only one locality, his W-1 (Russell, *op. cit.*), which has been subsequently destroyed and/or covered by slumping. From its location, W-1 should be one of the older localities on the North Fork of the Flathead River. Ongoing studies of the older strata of the Middle Fork of the Flathead River show that unionid clams, including Russell's taxa, are

abundant in those strata. The presence of these unionids demands a through flowing river, probably to the east or southeast, draining the Kishenehn Basin during the time of deposition. Absence of unionids in younger strata strongly suggest that either the through flowing river ceased to exist, or, possibly, may have shifted to a westward direction. Strong seasonal variation in water levels during deposition of the upper strata could have resulted the local extinction of the unionid clams after the through flowing east-bound river either ceased, or drainage shifted to the west. This should be resolved by the ongoing study of the Middle Fork strata.

Summary.—Geology.—The Kishenehn basin is a narrow, normal-fault bounded basin which contains as much as 3,400–4,300 m of middle Eocene-early Miocene (ca. 49–20 Ma) synextensional sedimentary rocks of the Kishenehn Formation. Kishenehn sedimentation was rapid and concurrent with extensional movements on the bounding fault systems; the master fault system which controlled the basin-origin being west-dipping faults of the Flathead fault system. Thus, the Kishenehn Formation provides a record of the history of fault-displacements on the Flathead fault system and the tectonic and biologic evolution of the late Paleogene landscape of NW Montana and SW British Columbia. Systematic downdropping and rotation of Kishenehn strata along the Flathead listric normal fault imparted an eastward tilt to basal strata, a tilt that flattens upsection toward the northeast. The result of rapid and near-continuous sedimentation above an active listric normal fault system is a wedge-shaped sedimentary prism that is devoid of intraformation angular-unconformities or well-developed paleosols (i.e., unconformities with long hiatuses in sedimentation). Although the age-record of Kishenehn deposits spans over 25 m.y., our study of Kishenehn mollusks in the North Fork of the Flathead River sampled only a limited age range, mainly Chadronian. The reason for this is that the river weaves a course only slightly oblique to the axis of the Kishenehn basin. Therefore because of rapid Kishenehn sedimentation rates, only a limited amount of geologic time is represented by the fossil localities examined along the river corridor. The fossil data, however time limited, are critical to reconstruction of ancient Kishenehn landscapes and provides insights into paleotopography, paleoenvironments and paleoecology of a rapidly evolving structural basin that was surrounded by mountain ranges.

Summary.—Paleontology.—The molluscan fauna of the northern Kishenehn Basin is exceptionally diverse. The 55 taxa recovered are more than twice as many as the next most diverse molluscan fauna, the Cabbage Patch l.f., of the Western Interior. Of the 55 taxa in this fauna, 32 are new, and described herein, and seven require changes in taxonomy. Four taxa are referred to living species, in that the shells of the fossil specimens are indistinguishable from those of living species. However, this does not necessarily imply that they are biologically identical.

Sympatric studies of 52 taxa (three taxa were deemed unusable for that study) of the northern Kishenehn Basin clearly showed the mixed nature of this molluscan local fauna, overall. Modern analogs of eight taxa (seven terrestrial, one aquatic) clearly require a moist tropical environment for survival, and are current residents of the Caribbean Basin and surrounding continents. These are the Group I fauna. The modern analogs of 18 taxa (16 terrestrial, two aquatic) are presently inhabitants of tropical/semitemperate semiarid environments. They are currently found in a broad band from the western Gulf of Mexico across northern Mexico and southern United States to Southern and Baja California. These comprise the

Group II fauna. Two taxa are found in both Groups I and II. The remaining analog taxa (15 terrestrial, 16 aquatic) generally fit into a moist, temperate group, Group III. They are most plentifully represented in the eastern United States, for which the general area of Kentucky could be considered the core of their range. Four of the analog terrestrial taxa and eight aquatic analogs included in this Group trend towards a western distribution. However, the climatic requirements of these western terrestrial analogs are sufficiently similar to warrant their inclusion in Group III. Three of the terrestrial analogs of Group III overlap into Group II climatic zones.

The degree of extralimitality displayed by mollusks of the northern Kishenehn Basin l.f. follows the pattern suggested by the other molluscan faunas of the Western Interior, i.e., pre-“Terminal Eocene Event” (TEE) faunas have a greater extralimitality (Table 8, 50% or greater), while post-TEE faunas have greater endemism. In the case of the Kishenehn Basin l.f., all (100%) of the Group I and II analogs are displaced latitudinally (south). The Group I analogs are generally displaced by 20°–30° of latitude (2,200–3,300 km) to the south, with a strong east component included, whereas the Group II analogs are displaced by 10°–20° of latitude (1,100–2,200 km) to the south with less or no eastward component. Most Group III analogs are displaced only longitudinally (east-west) into areas of greater MAP. Although the core of their present ranges may be distant, many of these taxa can still be found in northwestern Montana, albeit only in isolated favorable habitats at the limits of their modern range. Typically, the Group III displacement is sufficient to insure 150% to 200% of the current MAP in the Kishenehn Valley (Polebridge, MT, 57.2 cm/yr, see Fig. 2).

The molluscan fauna of the northern Kishenehn Basin l.f. is of late Eocene-early Oligocene age, occurring primarily during the Chadronian and Orellan NALMA's. However, the three Groups within this fauna permit inferences to be made covering a wider time span. The Group I tropical fauna is a relic of the tropical Uintan-early Duchesnean NALMA's that preceded the Middle Eocene Event, an episode of strong global cooling that occurred during the middle Duchesnean NALMA. The Group II semiarid fauna developed during the drier, and somewhat cooler, climate of the late Duchesnean-Chadronian NALMA's. The Group III temperate fauna was developing in the eastern highlands, bordering the Kishenehn Basin, during the Chadronian NALMA. The early presence of taxa of this Group, in association with Group I and II faunas, was probably a result of transportation in runoff from these eastern highlands (McMechan, 1981; Constenius, 1982). However, as further cooling occurred, leading into, or during the “Terminal Eocene Event”, Group III taxa rapidly colonized the lowlands previously occupied by the Group I and II faunas.

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Appendix—*Molluscan Fossil Localities, Kishenehn Basin, Montana North Fork of the Flathead River.*

Locality	Name	Latitude	Longitude
<i>British Columbia Localities</i>			
CMC-1	Commerce Creek	49 08'15"	114 29'12"
Locality CC46 of McMechan, 1981.			
Age: Late Eocene, ?Duchesnean to middle Chadronian.			
North bank of Commerce Creek, 1.0 km west of Middlepass Creek road.			
NFF-1	E-5	49 07'46"	114 29'47"
Locality E-5 of Russell, 1964.			
Age: Late Eocene, ?Duchesnean to middle Chadronian.			
East bank of Flathead River, 1.0 km north of Sage Creek road bridge.			
NFF-2	E-4	49 07'17"	114 29'38"
Locality E-4 of Russell, 1964.			
Age: Late Eocene, Chadronian.			
East bank of Flathead River, immediately north of Sage Creek road bridge.			
NFF-3	E-3	49 02'41"	114 29'44"
Locality E-3 of Russell, 1964.			
Age: Late Eocene, middle to late Chadronian.			
East bank of Flathead River, 1.0 km northeast of Canadian Kootenay Oil Company (d-41-A/82-G22) oil well derrick road.			
NFF-4	Island	49 02'01"	114 30'00"
Age: Late Eocene, late Chadronian.			
Small island in Flathead River, 3.5 km north of International Boundary.			
NFF-5	W-2	49 01'44"	114 30'25"
Locality W-2 of Russell, 1964.			
Age: Late Eocene, middle to late Chadronian.			
Cut bank 350 m west of Flathead River, 1.25 km south of mouth of Couldrey Creek.			
NFF-6	E-2	49 01'18"	114 29'35"
Locality E-2 of Russell, 1964.			
Age: Late Eocene, late? Chadronian.			
East bank of Flathead River, 2.1 km north of International Boundary.			
NFF-9	Moose City North	49 00'36"	114 28'57"
Age: Late Eocene, late? Chadronian.			
West bank of Flathead River, 500 m north of International Boundary.			

Montana Localities

NFF-10	Moose City South	48 58'34"	114 26'44"
Age: Late Eocene, Chadronian.			
West bank of Flathead River, 2.25 km south of International Boundary.			
NFF-12	Starvation Bend	48 55'39"	114 23'14"
Age: Late Eocene, Chadronian.			
West bank of Flathead River, 1.0 km south of mouth of Starvation Creek.			
NFF-17	Kintla Creek/River	48 54'48"	114 22'33"
Age: Late Eocene, ?Duchesnean to Chadronian.			
East bank of Flathead River, north side of Kintla Creek at mouth.			
KTL-1	Kintla Creek/CMNH	48 55'04"	114 26'05"
Age: Late Eocene-early Oligocene, late Chadronian-Orellan.			
North side of Kintla Creek, at crossing of Inside North Fork Road.			
NFF-18	Lower Kintla Rapid	48 54'30"	114 22'23"
Age: Late Eocene, Chadronian.			
East bank of Flathead River, 1.0 km south of mouth of Kintla Creek.			
NFF-19	Wurtz Bend	48 54'05"	114 22'35"
Age: Late Eocene, ?Duchesnean to Chadronian.			
East bank of Flathead River, west of Wurtz Landing Strip.			
NFF-21	North Ford Creek	48 52'59"	114 21'55"
Age: Late Eocene, Chadronian.			
East bank of Flathead River, 2.5 km north of mouth of Ford Creek.			
NFF-23	South Ford Creek	48 52'30"	114 21'51"
Age: Late Eocene, Chadronian.			
East bank of Flathead River, just north of mouth of Ford Creek.			
NFF-26	Hook	48 51'12"	114 20'52"
Age: Middle to late Eocene, Duchesnean to early Chadronian.			
East bank of Flathead River 800 m north of mouth of Whale Creek.			
BWN-2	Bowman Creek	48 47'55"	114 14'25"
Age: Late Eocene, Chadronian.			
North bank of Bowman Creek, 3.0 km from mouth on Flathead River.			